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MORPHOMETRY AND HYDROGRAPHY OF SOME NATURAL LAKES OF THE NORTH CAROLINA COASTAL PLAIN: THE BAY LAKE AS A MORPHOMETRIC TYPE

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INTRODUCTION

In the summer of 1947 under the sponsorship of the North Carolina Wildlife Resources Commission studies were begun on a number of natural lakes in Bladen and Columbus counties.[1] It was realized at the outset from the examination of airplane photographs of the region and from reading the theories by various geologists concerning the origin of the Carolina bays that these lakes probably were of the same origin. It was not entirely unanticipated, therefore, to discover that the lakes are surprisingly alike in many of their morphometrical, chemical, and even biological characteristics, enough so to warrant considering the Bay Lake as a morphometric type. The present paper is concerned primarily with the distinctly morphometrical features of the lakes and to a lesser extent with some of the chemical characteristics of their water. It presumes to furnish a basis for further hydrobiological studies.

In the Atlantic Coastal Plain from Virginia to Georgia there are thousands of shallow, elliptical or ovoid depressions known as "Carolina Bays" from their first having been studied in the Carolinas where they are most abundant, and from their containing the various species of bay trees—*Magnolia virginiana*, *Gordonia lasianthus*, *Persea borbonia*, and *Persea palustris*. Strangely enough there have been very few published studies on these bays aside from geological investigations to determine their origin and botanical studies on their vegetation; but judging from the findings of Buell (1946) on Jerome Bay and current

[1] Other persons participating in the collection of the data here reported were Edward E. Hueske and T. Stuart Critcher of the N. C. Wildlife Resources Commission and A. Carter Broad of the Fisheries Research Institute of Morehead City. The Wildlife Resources Commission has also assisted in the publication of this paper by furnishing the plates of the illustrations.

investigations by the author on others, it seems likely from the nature of the sediments that many of these basins, perhaps all of them, at one time contained lakes. Nearly all such bodies of water have been extinguished by processes of filling in and lowering of the water table attendant on the incision of streams into the Coastal Plain, leaving behind the oval-shaped swamps so prominent from the air. But in North Carolina a small number of bay lakes still exist, with the main concentration in Bladen County in the vicinity of Elizabethtown.

As soon as the Carolina Bays were recognized by the geomorphologists, a number of theories were advanced to account for their origin, of which two are held most widely at present. Melton and Schriever (1932) proposed that all these depressions were formed by the impact of meteorites in the unconsolidated sediments of the Coastal Plain. As evidence accumulated the theory was modified in various ways, until in its present form it conceives of a large shower of meteorites striking the earth obliquely from a northwest direction, excavating the depressions not so much by the impact of the meteorites themselves or by their explosions on striking the earth as by the shock waves preceding them. (This whole subject is reviewed by Johnson, 1942.) Opposed to this theory is that of Johnson (1942), who conceived of the Coastal Plain depressions as having arisen from a complex of natural forces resulting from ground water, artesian water, solution, and wind action. The present paper does not attempt to decide what the most likely origin of these basins is, but merely to describe the present configuration of some of those still containing lakes and to consider some of the forces which have been active in producing them.

METHODS

From aerial photographs of the region made under the direction of the U. S. Department of Agriculture in 1938, working outlines of the lakes were traced. Actual surveying of the lakes was then completed with a plane table and a non-telescopic alidade. Stations (frequently cypress trees in shallow water close to shore) were established at convenient distances and were then incorporated into a triangulation grid with the plane table. A base line distance between two stations was measured with a standard 100-foot steel surveyor's tape.

As an outboard motor boat was run along ranges at a suitable relationship to each plane table station, soundings were made at convenient intervals of approximately 250 to 1000 feet, with a standard stadia rod, to the bottom of which was securely fastened a small tin can to enable the depth of water to be more accurately determined and to enable a sample of the uppermost sediments to be raised to the boat for examination. Data on the depth of water to the nearest tenth of a foot and the character of the bottom sediments were recorded at each position, which, after a suitable exchange of flag signals between boat and shore, was sighted on the range line with the alidade.

It was soon discovered that the major portion of these lakes was relatively flat, with most of the contour lines crowded close to shore. In order, therefore, to determine the bottom configuration more exactly, soundings were taken at

measured intervals of 50 or 100 feet, depending on the size of the lake, along numerous lines at right angles to the shore, extending from the edge of the water out to the central plain of the lake (Table 1).

In the laboratory the data from the field notebook were transferred to the plane table map, and contour lines at intervals of one foot were drawn by inspection. The areas of the lakes and of the various contour surfaces were measured with a K & E compensating planimeter. Volumes were then calculated by use of the established formula for this type of work, $V = \frac{h(a_1 + a_2 + \sqrt{a_1 \cdot a_2}}{3}$, where a_1 is the area of the upper contour surface, a_2 that of the lower, and h the vertical distance between them. For the lowermost portion, the formula for the volume of a cone was used, $V = \frac{h \cdot a}{3}$. Length of shoreline was determined with a standard map measurer. The shoreline development, which is the ratio of the

TABLE 1

Number and intensity of soundings in each of the six bay lakes investigated

LAKE	NUMBER OF SOUNDINGS			
	From plane table	Measured from shore	Total	Per mi.² lake area
Jones	87	131	218	623
Salters	99	244	343	700
Singletary	119	324	443	498
White	274	266	540	323
Black	242	114	356	162
Waccamaw	257	245	502	36

actual length of the shoreline to that of the circumference of a circle with an area equal to that of the lake, denotes the irregularity of the shoreline and the departure of the lake from a circular shape. Volume development which is equal to $3 \times \frac{\text{mean depth}}{\text{maximum depth}}$ indicates the general configuration of the lake basin according to whether the ratio is greater than or less than unity.

Only three types of bottom sediments were found in contact with the water: 1) *sand*, usually fairly clean and coarse in shallow water, becoming finer and darker with organic matter away from shore, 2) *pulpy peat*, a soft homogeneous, black or slightly brownish organic sediment, often containing a very small proportion of sand, detectable by rubbing some of the material between the fingers, and 3) *fibrous peat*, a light yellowish-brown mass of softened and partially decomposed rootlets, twigs, and leaves, with larger pieces of wood mixed in. The boundary between sand and either of the two other types of deposits was fairly sharp. That between pulpy peat and fibrous peat was not always sharp, so that the arbitrary limits of these two deposits may be subject to some variation according to individual interpretation.

RELIABILITY OF RESULTS

Sometime after the summer of 1947 it was discovered that three of the lakes—White, Jones, and Salters—had been previously surveyed in the late twenties by Thorndike Saville, Chief Engineer of the Water Resources Division of the North Carolina Department of Conservation and Development. By means of standard traverse surveys outlines of the lakes were prepared from which the area and length of shoreline were determined. No hydrographic studies were made. A comparison of the results in Table 2 reveals a close correspondence between the two sets of surveys. With respect to area the maximum difference is just over two per cent, and with respect to length of shoreline four per cent. The similarity in the figures for White Lake is especially interesting, because the outline map of this lake had to be pieced together from two separate aerial photographs. Because of the greater ease in making a plane table survey based on an outline obtained from aerial photographs, it is gratifying to learn that

TABLE 2

Comparison of area and length of shoreline determinations in two separate surveys

LAKE	AREA			SHORELINE		
	1947 survey	Traverse survey	Difference	1947 survey	Traverse survey	Difference
	acres	*acres*	*per cent*	*miles*	*miles*	*per cent*
Jones	224	227	1.4	2.19	2.27	3.7
Salters	315	322	2.2	2.70	2.73	1.1
White	1068	1065	0.3	4.77	4.58	4.0

this type of survey can be quite reliable for fairly large lakes as well as for small lakes.

In 1935 the Resettlement Administration in the process of developing Singletary and Jones lakes for recreational purposes determined the elevations of the lake surfaces[2] and prepared rough hydrographic maps, which agree in general with the ones reported in this paper. The accuracy of the maps presented in this report depends on how nearly the boat was on the range being worked at the time each sounding was sighted from the plane table. Since readjustments were frequently made in the boat's direction to correct for drift, using the stadia rod as a sighting device for making these adjustments, it is believed that most soundings were taken within 25 feet of the line being run. Allowing for the most acute angles sighted, it is probable that the true locations of each sounding is within 40 feet of where its position is plotted on the map. This difference is of little importance in the flat central plain of the lakes. The contour lines along shore where the gradient is steepest were located more accurately by measurement from shore. Hence, it is believed that the volume determinations from the contour maps are at least as accurate as the outline maps of the lakes.

[2] Surface elevations: Singletary 63 ft., Jones 73 ft. The elevations of the other lakes are probably less than that of Jones because of the general seaward slope of the Coastal Plain terraces.

GENERAL CONSIDERATIONS OF THE INDIVIDUAL LAKES

Jones Lake[3]

The smallest of the lakes investigated is one of the most attractive. Its dark colored water is virtually free of suspended matter, enabling a number 20-mesh plankton net to be towed for long distances without any appreciable decrease in efficiency.

Towards the southeast end where a natural sand beach occurs is a Colored Recreation Area, operated by the Department of Conservation and Development. No other cultural developments occur on the lake.

Jones Lake, as is typical of all the bay lakes, gives clear evidence of considerable fluctuation of water level during the past few hundred years. Along the east shore just north of the outlet, for example, is a row of cypress trees about 50 feet from shore, exactly paralleling the shore with 3 scallops. This represents an old shoreline, since the cypresses must get started on dry land. These trees are at present in 16 inches of water, which means that the lake level must have been approximately 16 inches lower at the time the trees became established than it is now. Although the trees are not very large, cores taken with an increment borer indicate they are approximately 400 years old. Along the deeper northwest shore are a few large isolated trees occurring in even deeper water, and hence presumably older, although not necessarily so. They give evidence of a lower water level.

Salters Lake

The least accessible of the lakes, Salters, probably has least reason for the average person visiting it. Fishing is poor, the shores of the lake are crowded everywhere with a dense, all but impenetrable tangle of shrubs and trees, and there are no natural sand beaches. There are no developments of any kind on the lake, except for a few boats which the Forest Service maintains for the use of the infrequent fishermen. The shoreline gives considerable evidence of somewhat recent expansion of the lake area.

Singletary Lake

Singletary boasts a greater length of natural sand beach than any of the other lakes of Bladen County. At the east end of the lake just below the outlet is a development begun by the Resettlement Administration and now operated by the Department of Conservation and Development as a group recreation camp. This is the only development on the lake.

The Resettlement Administration dredged out a channel in the outlet creek and constructed a spillway dam 160 yards from the original shoreline in the region of the sand rim. This provides a convenient reference point for observing fluctuations in lake level. On July 14, 1947, the lake level was 10 inches

[3] The diagrams of hydrography and distribution of bottom deposits and the morphometrical data for each lake at the end of the paper (Figs. 6–11, and Tables 8–13) should be referred to.

below the crest of the spillway, and on November 16, 1947, it was 4 inches above, giving an observed fluctuation of 14 inches. According to reports this is fairly typical of annual fluctuations in water level of all the Bladen County lakes.

Singletary Lake exhibits more filling in of the bay along the sides than do the others, yielding a body of water more elongated in shape than is the usual condition. As a result the shoreline development of Singletary is the largest of any of the lakes. The deepest water found in any of the lakes was near the southeast end of Singletary. The water of this lake contains a large amount of organic detritus which quickly coats anything placed in the water and clogs even a number 10-mesh plankton net so that its filtering efficiency is greatly reduced.

White Lake

White Lake derives its name from the clarity of its water and almost complete absence of color, a characteristic not shared by any of the other lakes. A white secchi disc is readily visible on the bottom, even in the deepest part of the lake. This feature has made the lake most desirable from a recreational standpoint, and has resulted in a number of resorts and many cottages being located along its shores.

The most plausible explanation for the lack of color is that of drainage. All the lakes except White Lake have their outlets somewhere in the southeastern to southwestern section, so that rainwater leeching through the bay vegetation and peat deposits at the northwest end must flow through the lake to leave the basin. In White Lake, on the other hand, the outlet is at the northwest end almost in the middle of the filled in portion of the bay, and hence the dark colored water from this region is drained away from the lake rather than through it. On November 15, 1947, for instance, after a rather heavy rain, the color of the water immediately adjacent to the northwest shore was as usual less than 10 parts per million, as measured with a USGS color set, whereas that of the outlet creek at the road bridge just outside the edge of the bay was 440 parts per million. At this same time there was a zone of colored water up to 100 yds. wide along the entire shore except at the northwest. The color of this zone ranged from 32 to 55, being darkest immediately adjacent to the shore.

According to reports White Lake is spring fed. Offshore about the middle of the northeast side are a number of round clean areas in a region where the sand is thinly covered with fine dark detritus. Careful soundings of these areas showed the centers about 8 inches lower than the edges, but the bottoms were hard, no bubbling as reported by other visitors could be observed through a water glass, and there was no detectable chemical evidence of any volume of water entering the lake through these depressions. Earlier in the year at a time of higher lake level and more favorable ground water conditions there might be visible evidence of inflowing water.

There is also a belief that some springs at the base of a cliff along the Cape Fear River within 3 miles of the lake are the result of an underground outlet from the lake, but there is no concrete evidence in the matter. The only known outlet is the small surface creek at the northwest end of the lake, which flows except in extremely dry periods.

Black Lake

Black Lake differs from the others in the indefiniteness of the margin of the bay in which it is situated. The others all have a distinctly oval outline, but that of Black Lake is quite irregular and in places appears to merge indistinguishably with neighboring bays. There are no natural sand beaches on the lake except at two small places along the southwest shore where the basin of Black Lake has cut across the sand rim of a smaller bay during its period of enlargement. At the southeast end of Black Lake are many small irregularities in the shoreline, with adjacent small coves being separated by narrow peninsulas of land often only a few feet wide, covered with typical bay shrubs and trees. This condition seems to represent a fairly recent expansion of the lake area through erosional activities. This is a phenomenon apparent in several of the other lakes as well, particularly Salters and parts of Singletary.

Black Lake, although the largest natural lake in Bladen County, is likewise the shallowest, with the maximum depth of water being just over seven feet near the southeast end.

An unknown quantity of water drains into Black Lake bay through a small inlet towards the northeast end. This is not readily detectable from the lake, but is apparent at a nearby road bridge. The outlet from the lake at the south end has no definite channel but rather spreads somewhat diffusely over and through the surface of the ground, resulting in a slow unidirectional drift of water through swampy land.

Black Lake is accessible only with difficulty by road and there is no cultural development of the lake.

Lake Waccamaw

Waccamaw, the largest of the lakes studied, is nevertheless smaller than the dimensions of five by seven miles claimed by the nearby inhabitants. The lake is more nearly three by five miles. The erroneous conception as to size dates back at least to the time of John Bartram, who reported in the diary of his journey in 1765–66, "... Wocoma lake ... is 8 miles long & 5 broad & about 12 foot deep & very shoal toward ye borders in some places ..." (Harper, 1942). The exaggeration of the horizontal dimensions does not apply to the vertical, since the maximum depth of the lake reported is substantially correct.

Waccamaw is the only bay lake examined thus far with sand completely around the shore. This has been brought about by a sand bar working across the northwest end and isolating the peat-filled portion which had formerly been in direct contact with the open water, as it still is in the other bay lakes. A similar alteration, although to a lesser degree, occurred at the southeast end of the lake. As a result there are just two types of bottom deposits—sand and pulpy peat—at the surface of the present lake basin.

The dark colored water is probably derived from the extensive swamp to the northeast of the lake which drains into the lake through Big Creek. The color of the water in this creek is much darker than that in the lake itself, where it has been observed to fluctuate considerably from one year to another (See the data of Aug. 23, 1947, in Table 14). Hubbs and Raney (1946), for instance,

reported that the lake when visited on March 30, 1941, had almost no perceptible color, yet a color averaging 160 ppm. was observed in the lake in 1947. These variations would considerably affect the rate of light penetration and the dependent photosynthesis. Fish from the creek are much darker in color than those from the lake, and the question arises as to whether or not there is a partial barrier here to the free exchange of individuals.

The greatest depth of water is not in the lake itself but in Big Creek within a relatively short distance of the lake. The creek bottom is separated from the lake by a sand bar sloping steeply on the creek side, covered by less than four feet of water at the deepest place. It is likely that the creek water below this sill can be effectively isolated from the lake, especially in spring and fall when its bottom temperature might be considerably below that of the lake.

At the outlet of Waccamaw is a low concrete spillway dam with a broad concrete apron, constructed some time ago to help regulate the water level of the lake. Several years ago when the dam washed out around the abutments, the lake level dropped approximately 2 feet, permitting the establishment of a new crop of cypresses in the shallow southeast shoals.

Except for a few widely scattered cottages, cultural development of the lake is confined to the high ground for several miles along the upper northeast side. At one low point in this region there is exposed an outcrop of the fossiliferous Duplin formation of Miocene age, overlying the dark phosphatic Cretaceous formation (Clark, 1912). Hence, one has here the somewhat novel experience of collecting tertiary marine fossils (corals, oysters, Crepidula, Pecten, Venus, sharks' teeth, etc.) from a fresh water lake. It is believed this calcareous Miocene formation plays a significant role in bringing the chemical reaction of Waccamaw water to neutrality, whereas in all the other lakes studied the water is very acid.

THE BAY LAKE AS A MORPHOMETRIC TYPE

A detailed comparison of the lakes and their respective bays reveals a number of interesting and significant similarities. Each lake is located in an oval area known as a "Carolina Bay," surrounded more or less by a rim of white sand which is most prominent towards the east and southeast sides. It is likely that these sharp outer limits of the bays represent the maximum size of the lakes at any time in their history. Furthermore, in all lakes except Black and Waccamaw the bay appears to be congruent with the drainage basin because of the lack of surface affluents. This means that except for an unknown quantity of water coming in below the surface of the ground, the water reaching the lake is largely that precipitated directly into the bay. The implications of this are a general scarcity of dissolved materials in the water, and, partly resulting from this low productivity and partly from a low level of allochthony, a very slow rate of sedimentation.

PATTERN OF FILLING IN

The areas of the bays vary from a minimun of 638 acres for Salters Lake to a maximum of 9801 acres for Wacamaw, but these acreages are no longer

the areas of the present day lakes. There has been a considerable amount of lake obliteration by the accumulation of peat deposits. These, as Buell (1939) has already pointed out, are best developed towards the northwest end of the bay, so that as the basin increases in ecological age the lake becomes displaced progressively towards the southeast end of the bay.

Except for Black Lake (see Table 3) there is an inverse relationship between the present size of the lake and the percentage of the original bay area which has been filled in. Thus, Jones Lake, the smallest, now occupies only 34 per cent of its bay, whereas Waccamaw, the largest, still fills 91 per cent of the area of its bay. It appears, however, that the small lakes are being obliterated more rapidly because of their original smaller size rather than because of a faster rate of areal decrease. The absolute areas of the various bays filled in appear to fall

TABLE 3

Areas of the bays and their contained lakes in Bladen and Columbus counties, N. C.

The bay area in all cases was taken to the outside edge of the typical bay vegetation where it meets the surrounding sand rim. The bay area for each lake does not include that of any overlapping bays, as in the case of Salters, White, and Black (see Figures 1 and 2).

LAKE	AREA		PER CENT OF BAY OCCUPIED BY LAKE	ACRES OF BAY FILLED IN
	Bay	Lake		
	acres	*acres*		
Jones	667	224	33.6	443
Salters	638	315	49.4	323
Singletary	1022	569*	55.7	453
White	1496	1068	71.4	428
Black	2361	1418	60.0	943
Waccamaw	9801	8938	91.2	863

* The lake area does not include that of the artificial channel at the outlet.

readily into two groups. In the four smallest lakes (and likewise the four smallest bays)—Jones, Salters, Singletary, and White—slightly more than 400 acres of the original bays have been filled in. The figure for Salters Lake is less than this average by almost 100 acres, but at the time of the survey it was noted that Salters had more of an erosional than a depositional shoreline, indicating that perhaps the area of this lake has been enlarged from a previous minimum. The two largest lakes—Black and Waccamaw—have had twice as much of their original areas extinguished, but these figures are probably likewise misleading, in that there is evidence that both lakes have been enlarging their basins in recent time. One would ordinarily expect a larger lake, because of its greater length of shoreline and greater volume of shallow water, to exhibit a greater absolute areal decrease in unit time than a smaller lake.

The apparently constant rate of areal decrease in four of these lakes may be largely coincidental. There are many bays in the Coastal Plain (see Fig. 1) larger than those containing the lakes which have been completely filled with

vegetation and peat deposits. Either the rate of filling in these bays has been considerably faster than in the lake bays, perhaps varying with the original depth of the basin, or the filled-in bays represent older basins. Studies to determine the ages of a number of these basins have not yet been completed.

As the basins have been filled in, the lakes have not only been displaced towards the southeast, but two other phenomena have taken place concurrently: 1) the general shape of the lake (except for Singletary) has tended to become

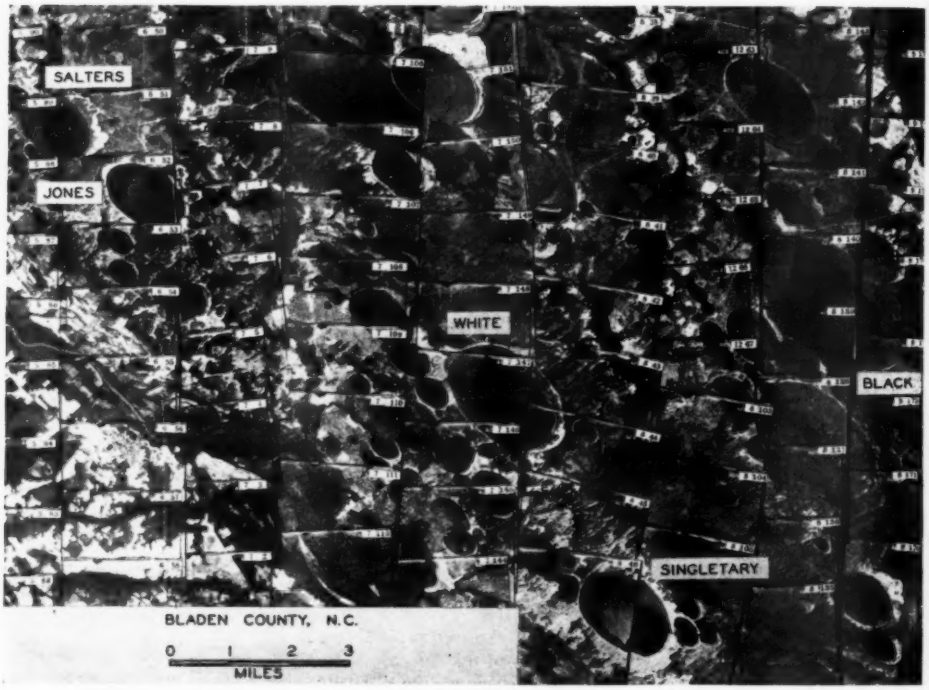

FIG. 1. Photographic mosaic of a portion of Bladen County, showing the location and general relationships of five bay lakes. (USDA, Production and Marketing Administration.)

more nearly equidimensional than the original bay, and 2) the axis of elongation of the lake has rotated clockwise with reference to that of the respective bay (see Figs. 1 and 2).

Table 4 shows that the length-width ratios of the lakes are in all cases except Singletary less than those of the respective bays. Singletary Lake is relatively more elongate than its containing bay, a condition which has been brought about by means of a relatively greater degree of areal decrease along the northeast and southwest sides than at the northwest end. The greatest change in relative

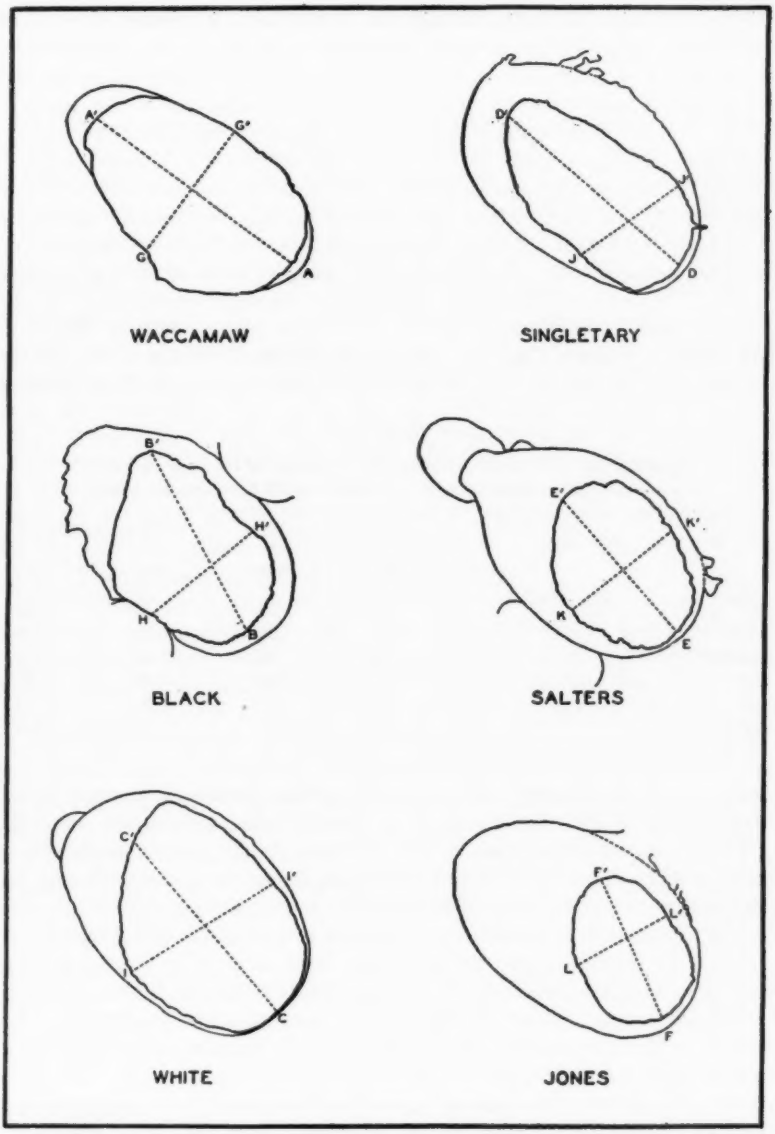

FIG. 2. Reduction of the bay lakes and their containing bays to the same absolute size to show the general pattern of orientation and filling in.

dimensions is in Waccamaw, where there has been filling in at both ends but none along the sides.

The directions of maximum elongation of the bays and lakes shown in the table are only approximate, since there was no means in the field of determining true north nor of determining the axes of elongation. Instead the angles listed were measured from the index maps of the aerial photographs of the region (see Fig. 1). Hence, these determinations are subject to any errors produced in assembling the photographic mosaic and to individual error in determining just what are the axes of the bays and lakes. The latter would probably be greatest in the case of Singletary, where the shape of the bay is somewhat anomalous.

The values obtained by these measurements are nevertheless instructive in that they emphasize first of all the marked similarity in orientation of the Carolina Bays. Except for Singletary, the axes of the bays do not differ by more than 6 degrees. Considering only the four lakes, Jones, Salters, White, and Black, which are much alike, the amount of clockwise rotation of the direction of elongation of the lakes respective to their bays has been from 22 to 28 degrees.

TABLE 4

Approximate directions of maximum elongation of the bays and their contained lakes, and ratios of maximum length to maximum width

LAKE	DEGREES WEST OF NORTH		LENGTH/WIDTH RATIO	
	Bay	Lake	Bay	Lake
Jones	57	25	1.57	1.44
Salters	54	26	1.61	1.39
Singletary	46	42	1.53	1.97
White	51	26	1.46	1.46
Black	51	28	1.59	1.48
Waccamaw	56	56	1.73	1.50

Such a marked similarity in "behavior" has certainly been in response to some widespread force, and one is inclined to think of the predominant winds from the northwest to southwest quadrant. Johnson (1942) places considerable emphasis on these winds in his theory concerning the origin of the bays, and Buell (1939) believes that they have been primarily responsible for the observed pattern of basin filling, most pronounced towards the protected northwest shore. Evidence will be presented later to show that these winds have been of great importance in producing much of the present basin configuration and distribution of bottom deposits. Extrapolating, it seems reasonable that the wind-generated currents in the early history of the bays were important in determining the original shape and nature of the basins.

The extent of areal decrease can be readily determined from photographs, but the extent of volume decrease can be determined only with great difficulty by borings taken along longitudinal and transverse ranges. It is not yet known, therefore, whether or not the largest lakes were also the deepest, nor is it known why lakes have persisted in these few bays but have completely disappeared in the surrounding bays, many of which have a greater surface area (see Fig. 1).

Whatever the original depths, the present lakes are all shallow. Waccamaw is not even a foot deeper than Salters, although its area is almost 30 times greater.

BOTTOM DEPOSITS

An ordinary survey can determine only the sediments at the surface of contact with the water, or those immediately beneath the surface. At the surface of these lakes are sand, a yellowish-brown fibrous peat, and a soft "greasy" pulpy peat (dygyttja?). Fibrous peat occurs only in a relatively narrow zone along the shore at the northwest end where the bays have been filling in most rapidly. Sand occurs elsewhere along the shore from the edge of the shore down the slope to the flat bottom of the lake. In Waccamaw, as previously stated, bars of sand have cut off the peat deposits at the northwest and southeast ends of the bay, resulting in sand all around the lake; no fibrous peat was found in the lake bottom. In all the other lakes except Jones the sand overlaps the fibrous peat offshore at the south end of the fibrous peat zone, and in White Lake at the north end as well (see Figs. 7b, 8b, 9b, and 10b). This makes it appear that either the sand is gradually working around the northwest shore and may eventually result in a condition like that in Waccamaw at the present time, or that the fibrous peat is a more recent deposit which has been laid down over the sand. The latter alternative is more likely, because in a number of instances only 0.1–0.2 foot of fibrous peat was found overlying sand.

The boundary between sand and pulpy peat is usually sharp and can readily be determined with a sounding pole. The sand, however, in some places extends beneath the pulpy peat, and can be felt beneath a thin layer of the softer material. The Black Creek formation, in which the Bladen County lakes are located, is predominantly sand, so that it is likely the bottoms of the original basins are sandy in nature. The boundary between fibrous peat and pulpy peat is to a certain extent a matter of individual opinion, since there is more or less of a gradual change from the greasy pulpy peat of the central plain to the yellowish fibrous peat at the northwest end.

A fourth deposit which appears to underlie the pulpy peat almost everywhere except immediately where it comes in contact with the sand is a light gray (sometimes brownish gray) silt or clay. This deposit was not found at the surface anywhere, although in White Lake it was at times covered by only a foot of organic sediments.

In Table 5 the percentage which each of the three surface sediments comprises of the total lake bottom as projected on the surface area of the lake is given. Since sand and pulpy peat are the two most extensive deposits, there is naturally an inverse relationship between them: when one declines in amount the other increases, and conversely. When the lakes are arranged in order of increasing size, a natural series appears to result. The largest lakes possess the greatest proportion of sand and the least of pulpy peat, whereas the smallest lakes have the least sand and the most pulpy peat. This results in direct relationships between the composition of the bottom sediments, the present size of the lakes, and the percentage of the original basins filled in by peat deposits.

As the lakes increase in ecological age (become smaller through filling in of their basins), the quantity of sand in the bottom decreases and of pulpy peat increases. When the lake area has been reduced to such an extent that wave action can no longer keep the shores towards the southeast end clear of the finer sediments, sand is then entirely eliminated from direct contact with the water. Such a condition was not observed in the lakes examined.

The fibrous peat along the protected northwest shore has probably resulted from the trunks, branches, and leaves of the vegetation growing near the shore and overhanging the water for distances up to 12 feet falling into the water and sinking to the bottom. The relative amount of this deposit in a lake may well be an indication as to the rate of filling in, inasmuch as areal decrease is most important at the northwest end.

TABLE 5

Percentage composition of the lake bottom deposits, measured in terms of the surface area of the lake

LAKE	PER CENT OF TOTAL		
	Sand	Pulpy peat	Fibrous peat
Jones	21	71	4
Salters	26	59	15
Singletary	43	49	8
White	44	52	4
Black	48	45	7
Waccamaw	64	36	0

MORPHOMETRY OF PRESENT LAKE BASINS

Although the configuration of the original lake basins cannot readily be determined, that of the portions still occupied by water can be ascertained by making a sufficient number of soundings. For any basin the existing configuration is the resultant of all the erosional and depositional processes which have been operating since the basin was formed.

The six lakes studied are similar in their morphometric characteristics, exhibiting progressive variations which appear to be a function of the size of the lake. The lakes are all somewhat saucer-shaped, with most of the contours being relatively close to shore, and the central plain being a remarkably flat area, sometimes varying not more than one-half foot in depth for 2000 yards or more. It is not surprising, therefore, to find that the volume development ratios are all greater than 2, except in the case of Singletary Lake, showing a wide departure from a conical shape.

It is impossible to ascertain without making detailed borings what the depths of the original basins were, but it is interesting that even with the different rates of sedimentation which have probably taken place, the present depths of the lakes are very much alike. The lakes are all shallow, with maximum depths ranging from 7.1 ft. in Black to 11.8 ft. in Singletary, and mean depths from 5.3 ft. in Black to 7.6 in Waccamaw. There is a tendency, best developed in Single-

tary, White, and Black lakes, for the deepest water to be located close to the southeast end of the lake (see Figs. 8a, 9a, and 10a).

When the longitudinal and transverse sections of the lakes are examined (Fig. 3) it is apparent that the lakes have mature profiles, at least along the southeast shore. In all the lakes within 50 feet of the shoreline there is an initial drop of from 1.1–2.0 ft. which is produced by the smaller abundant waves against the shore. Then there follows a wave-built terrace, whose width is roughly proportional to the length of the lake. In Waccamaw, for example, the southeast terrace extends almost 1500 ft. from shore, in Black Lake 400 ft., and so on down to Jones Lake, which has a gradual slope from the edge of the water to the central plain with no terrace at all. White Lake does not follow this relationship, in that on the basis of length of lake, its terrace should be midway in size between those of Black and Singletary, whereas it is actually only about 50 ft. wide.

The presence of these terraces indicates that the waves against the southeast shores are strong and have been in operation for considerable periods of time. But since the length of each terrace is related to the length of the lake rather than the length of the containing bay, it is also likely that the terraces are equilibrium phenomena, which are altered as the dimensions of the lake are altered.

At the northwest end of the lakes there are no terraces. Here, where the dense growth of bay vegetation comes to the edge of the water, there are depths up to 5 feet at the water's edge. No influence of the wind is evident along this shore. Of all the lakes Singletary shows the most gradual rise in the bottom from the deepest place at the southeast end to the northwest shore, as a consequence of which it has the smallest volume development ratio.

The southwest and northeast shores are somewhat similar in profile in the three largest lakes, but in the three smallest lakes there is a marked asymmetry, with the average slope of the southwest shore tending to be steeper than that of the northeast. Waccamaw shows two terraces along the southwest shore and one broad terrace along the northeast shore, which has a number of irregularities in it. Black Lake exhibits a small terrace towards the southwest, and what might be considered a rather extensive deep water terrace towards the northeast. Although the level of this latter terrace is little above that of the central plain of the lake, it is composed entirely of sand rather than of pulpy peat. White Lake, which has the most nearly regular basin of any of the lakes examined, cannot be said to have any lateral terraces. The three smallest lakes may or may not have traces of terraces at the southwest, but all of them—even Jones—have narrow terraces at various depths along the northeast shore. Thus for the particular places in the lakes where the profiles were made, in Singletary the terraces occur at depths of 2.7–3.4 ft., 4.0–4.4 ft., and 5.5–6.0 ft., in Salters from 3.0–3.4 ft., and in Jones from 3.6–4.1 ft. The transverse sections show that even in the two latter lakes there is a tendency towards development of multiple terraces.

In the only other published study on a Carolina Bay, Buell (1946) likewise observed the development of multiple terraces along the northeast and southeast sides in Jerome Bay, a completely filled-in bay in the northwest corner of Bladen County. With a Davis peat borer he penetrated the sediments of the

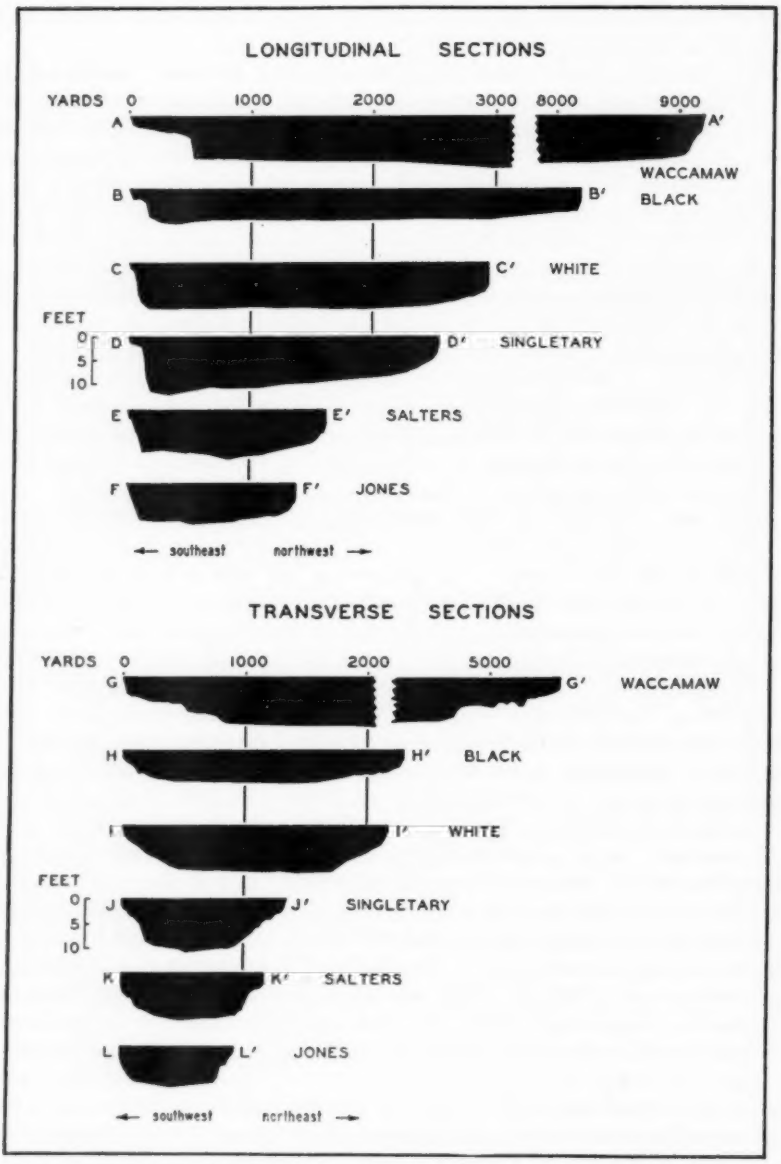

FIG. 3. Transverse and longitudinal profiles of the bay lakes. Note that the depths are greatly exaggerated with respect to the horizontal dimensions. The locations of these particular sections are shown in Fig. 2.

bay to the underlying sand, which was assumed to be the limits of the original lake basin. His study, however, is not strictly comparable to the present one, since from his profile diagrams it cannot be determined where the bottom was located at any particular stage of the lake, nor consequently how many of the terraces were exposed simultaneously.

It is difficult to conceive how along a single exposed shore a number of terraces might be formed simultaneously. Although the evidence from the terraces at the southeastern end is that these structures are in equilibrium with the wave action and hence can be modified in dimensions as the force of the wave action changes, it might nevertheless be true that the terraces along the northeast shore, not being subject to such strong waves, are more nearly permanent. They can possibly represent previous low water stages of the lakes. In each of the lakes, for example, there are cypress trees growing away from shore in water of varying depth, sometimes as deep as 4 feet. Whatever the depth at which these trees now occur, the lake bottom must have been exposed in order for the trees to get started, since cypress seeds cannot germinate and take root underneath the water. The fact that the terraces are best developed along the southeast and northeast shores indicates that the winds of greatest effect come from the northwest to southwest directions, as previously indicated.

At first consideration it seems anomalous that the rate of filling has been most rapid at the northwest end where the deepest water now occurs, and least of all at the southeast where the shallowest water of the entire lake is located. The northwest end of the original basin was undoubtedly shallow enough at one time so that vegetation could easily become established along this protected shore. Now, however, the water is so deep along this shore that only with extreme fluctuations in water level can new cypresses become rooted. The accumulation of fibrous peat offshore must be an extremely slow process.

New crops of cypresses do get started on the southeast and south shoals at the present time. A dense stand in White Lake in this region dates back about 130 years, presumably to the time when the lake level is reported to have been lowered about 2 feet by the operation of a sawmill at the east end, and in Waccamaw there is a more recent crop of new trees only a few years old, as previously indicated. No doubt there have been other similar stands in the long histories of these lakes, but for some reason—perhaps the strong wave action along this shore—the trees were eventually all killed without contributing materially to the advance of the shore into the lake. Thus the same forces which made the terraces and provided the best location for the establishment of new generations of trees are also responsible for keeping the trees off these shoal areas.

The aerial photographs of Lake Waccamaw are remarkable in that they were taken under conditions of water transparency and angle of sunlight enabling certain details of the terraces to be distinguished. The broad terrace at the southeast end is quite clearly visible, those to the northeast and southwest are a little less so, and each terrace has irregularities in it, which are in the nature of sand ridges formed by wave and current action.

At the southeast end of the lake for a distance of 6000 feet along shore are a

series of small ridges paralleling the shore and extending offshore for a distance of 1000 feet. These sand waves average 45 feet from crest to crest, but they are largest and farthest apart closest to shore where the currents are strongest.

Extending along shore for 11,000 feet from this zone towards the outlet of the lake are a series of ridges projecting out from shore at an angle towards the northwest (Fig. 4). They are not strictly parallel, because their direction of elongation tends to shift clockwise with increasing distance from the southeast end. These ridges are visible up to 1500 feet offshore, and in the area just north of the

FIG. 4. Aerial photograph of a portion of the south end of Lake Waccamaw, showing the prominent sand ridges in the terrace along the shore. (USDA, Production and Marketing Administration.)

outlet there is another more diffuse and irregular group of similar ridges extending up to 2500 feet from shore.

Along the northeast side of the lake are other sand ridges, which are quite irregular in shape, and trend in a direction slightly east of south. They are visible on the photographs up to 2500 feet from shore. The irregularities in the northeast terrace of Lake Waccamaw shown in Fig. 3 undoubtedly are produced by some of these ridges. No attempt was made to chart any of these bars and ridges on the hydrographic map.

Such extensive irregularities in the sandy bottom of Waccamaw indicate the force of the currents which can be generated by the winds. The ridges parallel to shore at the southeast end seem to indicate that the winds of maximum effect are from the northwest. Westerly and northwesterly waves reflected from the northeast shore have built up the irregular ridges trending southward. The

surface return of water at the southeast end appears to have been mainly clockwise, resulting in the extensive series of ridges along the south and southwest shore. If there is any general circulation of the lake generated by the winds, all evidence indicates that it is strongest in a clockwise direction. None of the

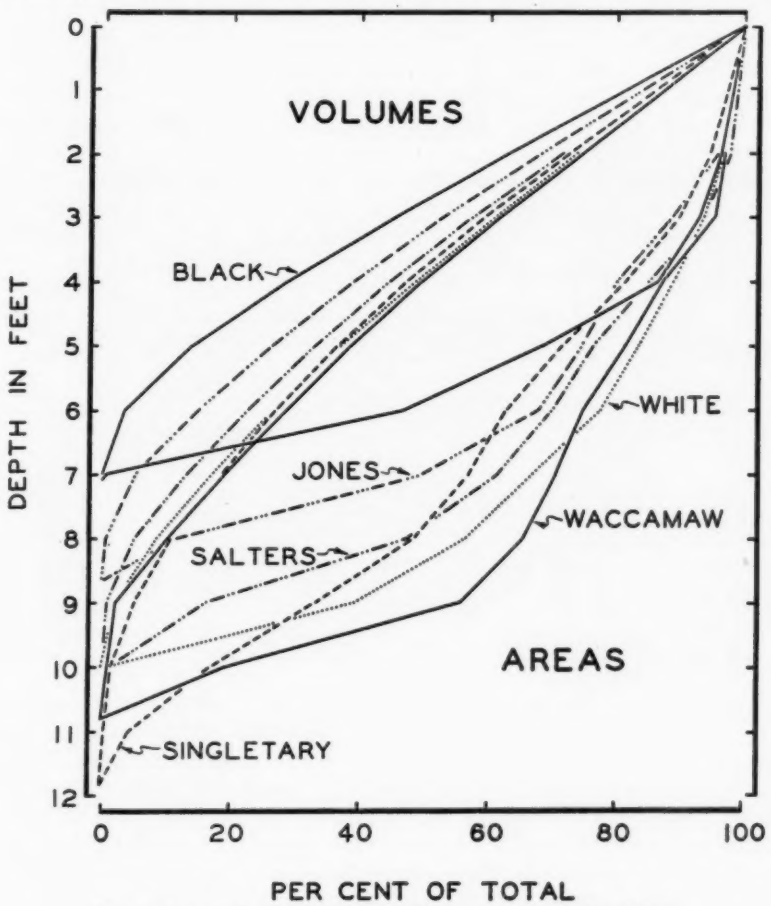

FIG. 5. Area and volume hypsographic curves for the bay lakes

other lakes, presumably because of their small size, exhibit similar sand bars, with the possible exception of Black Lake.

In biological studies on lakes it is frequently necessary to be able to determine the surface area at a particular depth, or the volume of water below a certain depth. Both of these types of data can be readily determined from the tables at the end of this report and from the area and volume hypsographic curves in Fig. 5. The area curves again emphasize the steep-sided, flat-bottomed shape

of the basins, and also demonstrate how little a fluctuation in water level of a foot or two would change the surface area of the lakes.

CHEMISTRY AND PHYSICS OF THE LAKE WATERS

Two vertical series of water samples and temperature measurements were obtained from each lake during the time it was being surveyed, and additional miscellaneous observations were made on the lakes in the fall of 1947 and the summer of 1948. The derived data, although inadequate to characterize these lakes completely, physically and chemically, do indicate a number of significant features concerning them.

Measurements of transparency were made with a standard 20-cm. secchi disc. Temperatures at the various levels were obtained by means of GM reversing thermometers. Water samples were obtained with a Kemmerer water bottle.

TABLE 6

Summary of average physical and chemical conditions in the six bay lakes during the summer and fall of 1947

LAKE	NUMBER OF SAMPLES	DISC	COLOR	pH	ACIDITY AND ALKALINITY		DISSOLVED O_2	
					ml. N/44 NaOH per liter	ml. N/44 H_2SO_4 per liter		
		ft.	*ppm.*				*ppm.*	*per cent*
Jones	9	2.4	297	4.34	10.7	3.0	5.7	70
Salters	7	1.8	299	4.49	9.9	3.2	6.0	71
Singletary	10	2.5	168	4.50	6.7	2.4	6.6	81
White	8	11+	<10	4.92	3.5	1.6	6.7	84
Black	6	1.8	182	4.40	7.6	1.9	6.4	82
Waccamaw	8	4.4	160	6.95	3.5	9.2	5.2	70

For oxygen determinations the "rapid sample-blank modification" of the Winkler method, as recommended by Ellis, Westfall, and Ellis (1946), was used. Saturation values were determined with the aid of the nomogram presented by Rawson (1944). Total acidity and alkalinity were determined by titrating separate 100 ml. samples with N/44 NaOH to the phenolphthalein endpoint, or with N/44 H_2SO_4 to the methyl orange endpoint. Ordinarily these results would be reported as parts per million of free carbon dioxide and bound carbon dioxide, but for reasons given later they cannot be so reported in the present instances. Hydrogen ion concentration was measured with a Coleman pH electrometer, Model 3D, standardized against an Hydrion buffer of value 5.6 ± 0.05. Color, expressed as parts per million of potassium chloroplatinate, was measured by visual comparison with a standard U. S. Geological Survey color set.

Table 6 summarizes the physical and chemical conditions in the lakes during the brief periods of observation, and Table 14 at the end of the paper presents the results of the individual series of analyses. It is apparent from these data that the penetration of light into the water, as measured by a secchi disc, is rather

low except in White Lake, where the disc was readily visible at the maximum depth.

One of the principal determinants of light penetration is the color of the water, which here varies from the almost colorless condition of White Lake to the strongly tea-colored water of Jones and Salters. The other three lakes exhibit an intermediate condition. Inspection of the table, however, shows that the correlation between color and transparency is only an approximate one, and the reason for this is that the amount of particulate matter (seston), both living and non-living, in the water, is the second important determinant of light penetration. Singletary, Black, and Salters lakes have greater quantities of non-living organic seston than the other lakes, which makes it possible, for example, for Jones and Singletary to have approximately the same transparency, even though the color of the former is almost twice as great. The evidence for the dark color being derived from the leaching of the vegetation and peat deposits around the margins of the lakes, and for the proposed explanation of the clarity of White Lake—that of drainage pattern—has already been discussed. Because of the pronounced color, all the lakes except White Lake would be considered dystrophic. Dissolved color accentuates biological and thermal stratification through its affect on light absorption, and these in turn tend to make the chemical stratification sharper than in a clear water lake.

The chemical reaction of most natural waters occurs within the pH range 6.0–8.5. If the acidity is great enough to lower the pH below 5.5, the acid condition can begin to affect biological processes and the lake is no longer harmonic: it is considered to be acidotrophic (Naumann, 1932). All the bay lakes here described, except Waccamaw, are strongly acidotrophic, with the average pH ranging from 4.34 in Jones to 4.92 in White. The higher pH (6.95) in Waccamaw is believed to result from the solution of lime and other minerals from the outcrops of the calcareous Duplin formation and of the older Cretaceous formation along the northeast shore (Clark, 1912).

Acidity in natural waters is usually caused by the carbon dioxide complex and/or organic acids such as humic acids dissolved in the water. Both of these can be eliminated as the primary cause of acidity in these lakes. If the pH of a fresh sample of water is determined, and then, after any free carbon dioxide present has been removed by thorough aeration, the pH is measured a second time, there is no consistent observable change in the pH value, showing that free carbon dioxide if present is not materially affecting the acidity. Even boiling a sample of water did not significantly alter the chemical reaction. That organic acids, likewise, are not the cause of the high acidity is demonstrated by the fact that the pH of White Lake is almost as low as that of the other Bladen County lakes, even though its color is very much less. Color of the type found in swampy lakes, it might be added, is primarily caused by these organic acids.

Table 6 demonstrates further that relatively small quantities of standard alkali are required to adjust the reaction of these lake waters to the phenolphthalein endpoint, and that likewise only small quantities of standard acid are needed to increase the acidity to the methyl orange endpoint. This indicates

two conditions: 1) that the substances producing the acidity although rather intense in their activity are present only in small quantities, and 2) that there is relatively little buffer capacity in the water to resist changes in pH. In most natural waters the figures for N/44 NaOH in Table 6 would be listed as parts per million of free carbon dioxide, and half the values of the N/44 H_2SO_4 figures as bound carbon dioxide, the latter indicating roughly the total amount of calcium and magnesium present.

Frequently samples of bottom sediments brought to the surface had a faint odor of hydrogen sulphide, even though the water is apparently well aerated at all times. This suggested that perhaps free sulphuric acid might be the cause of the low pH, since it is known (see Ruttner, 1940, for example, or any textbook in bacteriology) that the colorless and red sulphur bacteria in lakes obtain their energy from hydrogen sulphide, with the ultimate release of sulphuric acid, which diffuses into the surrounding medium. Ordinarily this acid would react with various metallic ions in the water, but where the water is poor in dissolved minerals, some free acid might be expected.

Presumptive evidence that sulphuric acid produces the observed acidity is available from two sources. In the summer of 1947 Mr. Robert E. Short (1948) of North Carolina State College made chemical analyses on the bottom sediments of several lakes as part of a project supported by the North Carolina Wildlife Resources Commission. The materials to be analyzed were first extracted from the sample with a weak sodium acetate solution according to standardized procedures of soil chemistry. Then the approximate concentrations of sulphates were determined turbidimetrically, using barium chloride to precipitate the sulphate (Spurway, 1944). This method gives only the extractable sulphates rather than the total sulphates in the sediments.

According to these analyses the extractable sulphates in the bottom deposits of the four lakes investigated—Jones, Salters, Singletary, and White—are high, ranging up to 800 ppm. Only two samples out of the 22 analyzed contained less than 100 ppm., and the simple numerical average for all the samples was 360 ppm. Of the various ions tested for, sulphate was present in greatest concentration, and even allowing for considerable error in the method, there would still be an abundance of sulphates in the bottom deposits.

In the summer of 1948 Mr. Howard T. Odum ran some analyses on bottom sediments from Singletary Lake and water samples from several of the lakes.[4] The sulphate content of the water in White, Jones, Salters, and Waccamaw varied from 6.1 ppm. in Waccamaw to 7.9 ppm. in White. Because of certain errors which developed in the benzidine method employed, it is felt these results are only approximate, although of the correct general magnitude. Assuming that these results are substantially correct, that all the sulphate present is in the form of sulphuric acid, and that the acid is completely dissociated, the pH of a solution with 7 ppm. of sulphate would be 3.8, which is reasonable considering

[4] The work of H. T. Odum here reported was sponsored by a research grant to the author in 1948, Project C-50, from the Carnegie Foundation for the Advancement of Teaching.

the fact that the other substances present in the water would modify the chemical reaction.

Instances of low pH resulting from free sulphuric acid are reported in the literature. Yoshimura (1934) investigating Kata-numa with a minimum pH of 1.4 found 474 milligrams per liter of sulphate ions. Ohle (1934) reported that the Tonteich at Reinbeck contains significant quantities of sulphuric acid, but pointed out that an unusually high sulphate concentration is not necessary in a minerogenous acidotrophic lake, for example Pinnsee. Uéno (1934) reported that Onuma-ike had pH values of 2.8 to 3.8 over a five-year period. At one time he found the water contained 92 milligrams of sulphuric acid per liter.

These instances all occur either in regions of volcanic activity or in regions of iron pyrites oxidation. The North Carolina Coastal Plain is negative in both these respects. If the acidotrophy of this region is shown by additional work to result from sulphuric acid, it is likely that biological activity will have been the source.

The dissolved oxygen content of the lake waters never approached saturation, even in the surface waters. The particular analyses made showed White, Singletary, and Black lakes forming one group with approximately 80 per cent of saturation, the other three a second group at approximately 70 per cent. On the basis of biological productivity it was surprising for Waccamaw to have a lower average oxygen content than Black Lake, for example. The reasons for this are not known, since many factors would have to be studied concurrently to determine the controls of the oxygen levels at any particular time.

With the lakes as shallow as they are there is, of course, no permanent summer stratification. The chemical conditions from top to bottom may change over relatively short periods of time, depending on rainfall, photosynthesis, wind action, etc. Yet during bright, calm days steep microthermoclines can develop at the surface, temporarily cutting off the lower water from contact with the air. Such stratification, however, can be quite readily dispelled by the violent convectional squalls which often follow such conditions in the summer. In Black Lake on September 4, 1947, for example, the surface water temperature was 34.9°C, at one foot almost the same, and at 2 feet 31.0°C. A temperature difference of 5.5 degrees existed at this time between the surface and three feet. Surface conditions in Waccamaw on August 18 were almost as severe, with the temperature at the surface being 34.0° and at 3 feet 29.5°. The greatest temperature gradient found was in Salters Lake on June 30, 1947, with a temperature change of 5.7° over a vertical distance of 19 inches. The surface temperature at this time was 35.0°C. The examples quoted represent extreme conditions. Usually the temperature differences between surface and bottom were less than one degree centigrade.

Of the several chemical substances analyzed, only oxygen showed any consistent stratification. The tendency was for the per cent saturation to decline slightly with increasing depth, indicating that maximum oxygen addition through photosynthesis and agitation was occurring at or near the surface. In White Lake, however, the greatest concentrations of oxygen were in the bottom water,

which may well have resulted from photosynthesis by the higher plants growing on the bottom. White Lake was the only lake with rooted aquatics in deep water.

A few analyses were made by Odum on the amount of CaO in the lake waters, the total dissolved substances, and the loss on ignition. These data, summarized in Table 7, are subject to rather large errors and hence are only preliminary. The analysis of dissolved matter, for example, was made on 200 ml. samples, whereas with such small quantities of dissolved matter much larger samples should be used to reduce the relative magnitude of instrument errors. Calcium determinations were likewise made on 200 ml. samples, but here the quantities present are so small that errors up to several hundred per cent would not appreciably change the relative magnitude of the results. The general reliability of the latter results is evidenced by the small quantities of standard acid required to bring the reaction of these waters to the methyl orange endpoint (Table 6).

TABLE 7

Analysis of calcium and dissolved matter in the water of four bay lakes

LAKE	CaO	DISSOLVED MATTER		
		Total solids	Loss on ignition	Inorganic residue
	ppm.	*ppm.*	*ppm.*	*ppm.*
White	1.8	34.0	14.0	20.0
Jones	1.8	55.5	41.0	14.5
Singletary	2.1	53.5	39.0	14.5
Waccamaw	4.1	90.5	36.0	64.5

The quantities of calcium found in these lakes are very small. According to the system established by Naumann (1932) the lakes would be considered strongly oligotypic for calcium. In a study of 358 lakes in northern Wisconsin, Juday, Birge, and Meloche (1938) found that 21 per cent had a calcium content of less than 1 mg./l., and another 15 per cent 1.0–1.9 mg./l. This latter group would correspond to the North Carolina lakes, except for Waccamaw, which has a somewhat higher calcium content of 2.9 mg./l. To a considerable extent dystrophy develops only in regions low in calcium and magnesium, because these ions when abundant precipitate out the humic acids as humates, thereby preventing the accumulation of excessive color.

Loss on ignition, representing the dissolved organic matter, shows an expected correlation with the colors of the lake listed in Table 6. The inorganic residue in White, Jones, and Singletary is 20 parts per million or less, that in Waccamaw is three to four times greater. This agrees with the finding of a higher pH and a greater titratable alkalinity to methyl orange in Waccamaw than in the other lakes.

BIOTA

A separate report on the biota of these lakes will be presented later. Preliminary reports on the fishes (Hueske, 1948) and the benthos of Waccamaw (Frey, 1948b) have already appeared. A brief summary of these shows that in spite of the rather high acidity there is a rather good representation of organisms in the lakes. A total of 27 species of fishes were collected from the lakes. Waccamaw with 23 species had the greatest individual total, then followed White with 16, Jones with 13, Salters and Singletary with 12 each, and Black with 10 species. The lists contain a high proportion of predacious species, which, according to Hubbs and Raney (1946), explains the high rate of endemism in Waccamaw, where there were found three new species of *Fundulus*, *Boleosoma*, and *Menidia*, and possibly a new species of *Notropis* (described by Fowler). The fishes from the other lakes have not yet been sufficiently studied to determine whether or not evolution had proceeded along parallel lines in them.

The preliminary report on the benthos of Waccamaw showed an average of 579 organisms per square meter of bottom. The three groups of organisms most abundant were molluscs, 208 per square meter; two species of Tubificidae and one of Lumbriculidae, 179; and insects, 160, with *Hexagenia* nymphs being most abundant. The more acid lakes have smaller numbers of bottom organisms, particularly mollusca. In fact the only mollusc occurring in the acid Bladen County lakes is *Ferrissia hendersoni* Walker.

All lakes, except White, have a fairly good representation in the zooplankton of cladocera, copepods, and rotifers, but generally very little phytoplankton, as is to be expected in dystrophic lakes. Coker (1938) has already called attention to the fact that the plankton of White Lake is lacking in cladocera. Salters Lake was the only one with significant quantities of phytoplankton. Both in the summers of 1947 and 1948 *Asterionella* was abundant.

SUMMARY

The six lakes studied in the North Carolina Coastal Plain all conform to a common pattern, with differences resulting chiefly from differences in size of the basins. The lakes are saucer-shaped with regular outlines. Their single-depression basins are nowhere more than 12 feet deep, and the average depth varies from 5.3 to 7.6 feet.

Evidence from the pattern of filling, the profiles of slopes along the various shores, particularly the well developed terrace at the southeast end and the less well developed terraces along the northeast shore, the pattern of surface irregularities in the Waccamaw terraces, and the distribution of the bottom deposits all substantiate the marked influence of the westerly winds in controlling the morphometry and hydrography of the present basins, and presumably helping to shape the original basins.

The lakes tend to be dystrophic because of the swampy and peaty nature of their surroundings, but White Lake is colorless as a result of a difference in drainage pattern. The lakes tend to be strongly acidotrophic, with available evi-

dence indicating that sulphuric acid is very likely responsible for the low pH. The water of Waccamaw comes in contact with geological formations other than clean sand, from which it dissolves sufficient materials to raise its chemical reaction to neutrality. All the lakes are strongly oligotypic for calcium and have only small quantities of materials in solution. Presumably the basic pattern of production is oligotrophy, although no analyses on phosphorus and nitrogen are here reported.

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TABLE 8

JONES LAKE

Bladen County, N. C. 36°41'N, 78°36'W.

Area	224 acres	Maximum length	1420 yd., 0.80 mi.
Volume	707,100 yd.³	Length shoreline	3860 yd., 2.19 mi.
Maximum depth	8.7 ft.	Shoreline development	1.05
Mean depth	6.1 ft.	Volume development	2.10
		Number of soundings	218

DEPTH	AREA		STRATUM	VOLUME	
	Acres	Per cent of total		Yd.³ × 10³	Per cent of total
feet			*feet*		
0	224	100.0	0–2	0.71	32.0
2	214	95.5	2–3	0.33	15.1
3	198	88.4	3–4	0.31	13.9
4	181	80.8	4–5	0.28	12.7
5	167	74.5	5–6	0.26	11.7
6	152	67.8	6–7	0.21	9.6
7	111	49.5	7–8	0.10	4.7
8	26	11.6	8–8.7	0.01	0.4
Total				2.21	100.1

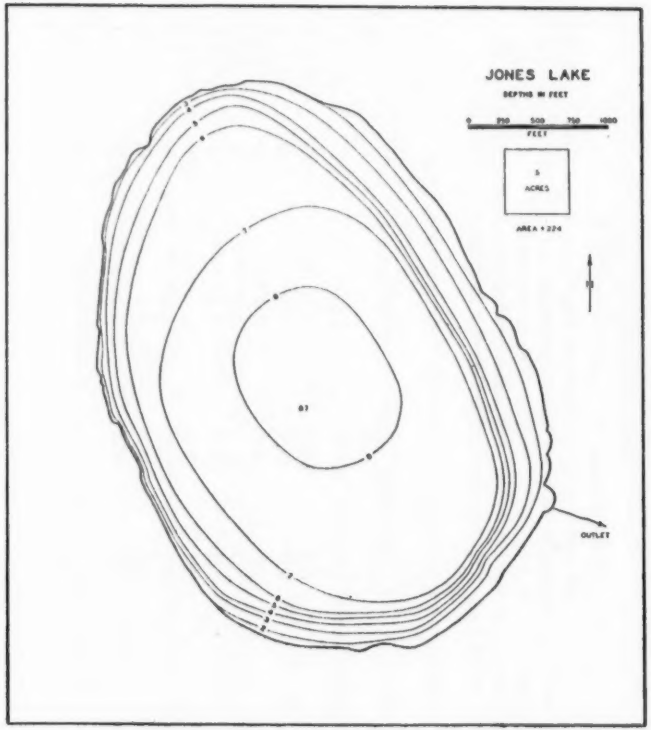
TABLE 9

SALTERS LAKE

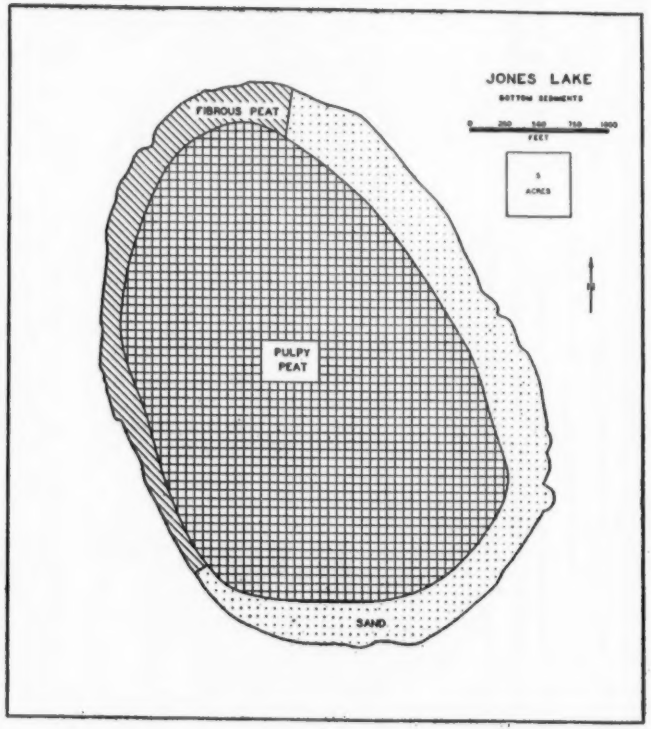
Bladen County, N. C. 36°42'N, 78°38'W.

Area	315 acres	Maximum length	1660 yd., 0.94 mi.
Volume	3,520,200 yd.³	Length shoreline	4760 yd., 2.70 mi.
Maximum depth	10.1 ft.	Shoreline development	1.09
Mean depth	6.9 ft.	Volume development	2.05
		Number of soundings	343

DEPTH	AREA		STRATUM	VOLUME	
	Acres	Per cent of total		Yd.³ × 10³	Per cent of total
eet			*feet*		
0	315	100.0	0–2	1.01	28.6
2	309	98.1	2–3	0.49	13.8
3	295	93.6	3–4	0.45	12.9
4	268	85.1	4–5	0.41	11.6
5	240	76.2	5–6	0.37	10.6
6	221	70.2	6–7	0.33	9.5
7	194	61.6	7–8	0.28	7.9
8	150	47.6	8–9	0.15	4.3
9	48	15.2	9–10.1	0.03	0.8
Total				3.52	100.0

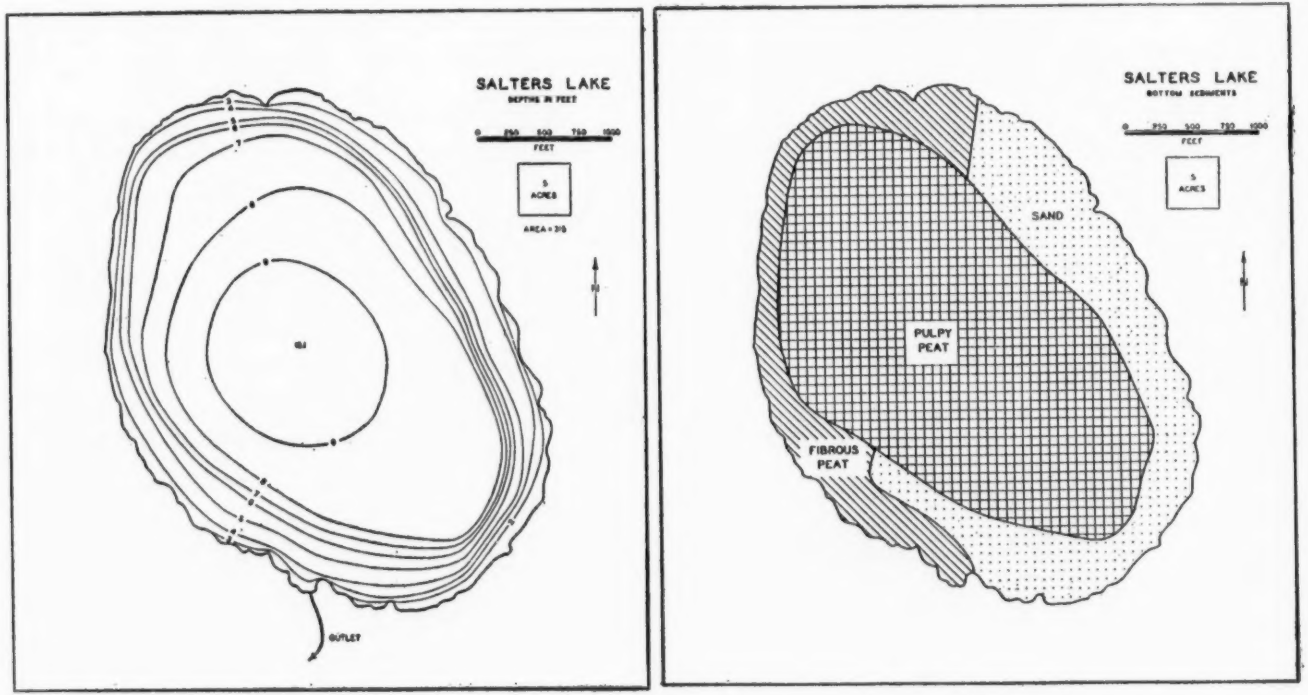


6a



6b

FIG. 6a and 6b. JONES LAKE. Hydrographic chart and distribution of bottom sediments.



7a 7b

FIG. 7a and 7b. SALTERS LAKE. Hydrographic chart and distribution of bottom sediments.

TABLE 10

Singletary Lake

Bladen County, N. C. 34°36′N, 78°28′W.

Area	572 acres	Maximum length	2630 yd., 1.49 mi.
Volume	6,495,300 yd.³	Length shoreline	6900 yd., 3.92 mi.
Maximum depth	11.8 ft.	Shoreline development	1.17
Mean depth	7.0 ft.	Volume development	1.78
		Number of soundings	443

DEPTH	AREA		STRATUM	VOLUME	
	Acres	Per cent of total		Yd.³ × 10^6	Per cent of total
feet			*feet*		
0	572	100.0	0–2	1.80	27.6
2	541	94.6	2–3	0.85	13.1
3	513	89.8	3–4	0.79	12.1
4	465	81.3	4–5	0.70	10.9
5	409	71.6	5–6	0.62	9.5
6	358	62.6	6–7	0.55	8.5
7	326	57.0	7–8	0.49	7.5
8	277	48.5	8–9	0.37	5.8
9	190	33.2	9–10	0.23	3.5
10	96	16.8	10–11	0.09	1.4
11	24	4.2	11–11.8	0.01	0.2
Total				6.50	100.1

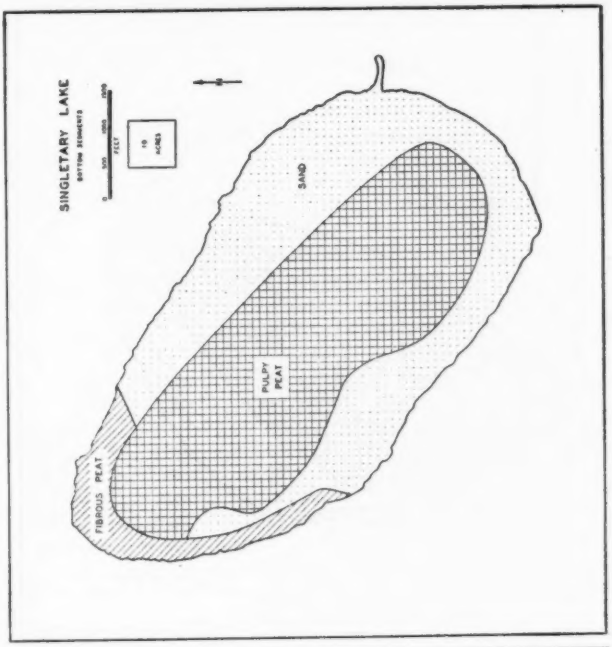
TABLE 11

White Lake

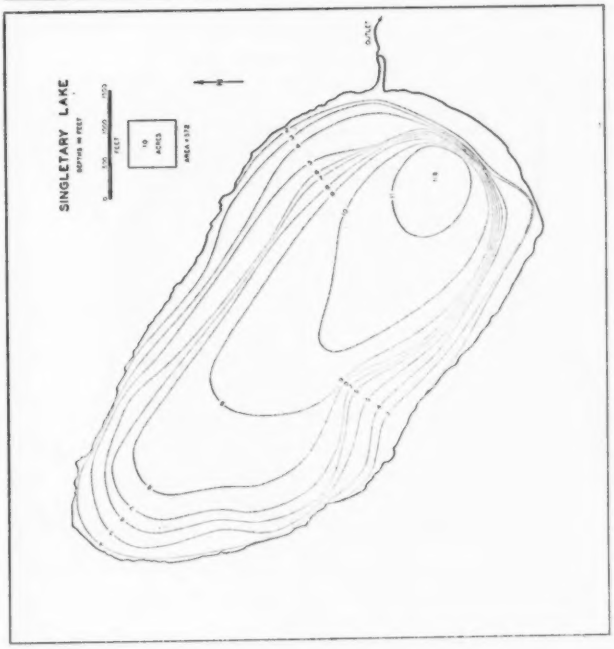
Bladen County, N. C. 34°39′N, 78°30′W.

Area	1068 acres	Maximum length	3190 yd., 1.81 mi.
Volume	12,844,100 yd.³	Length shoreline	8400 yd., 4.77 mi.
Maximum depth	10.6 ft.	Shoreline development	1.04
Mean depth	7.5 ft.	Volume development	2.12
		Number of soundings	540

DEPTH	AREA		STRATUM	VOLUME	
	Acres	Per cent of total		Yd.³ × 10^6	Per cent of total
feet			*feet*		
0	1068	100.0	0–2	3.39	26.4
2	1033	96.7	2–3	1.64	12.8
3	1001	93.7	3–4	1.57	12.2
4	947	88.6	4–5	1.48	11.6
5	892	83.5	5–6	1.39	10.8
6	827	77.4	6–7	1.24	9.7
7	712	66.7	7–8	1.06	8.3
8	604	56.5	8–9	0.82	6.4
9	418	39.1	9–10	0.25	2.0
10	5	0.5	10–10.6	0.002	0.01
Total				12.84	100.2

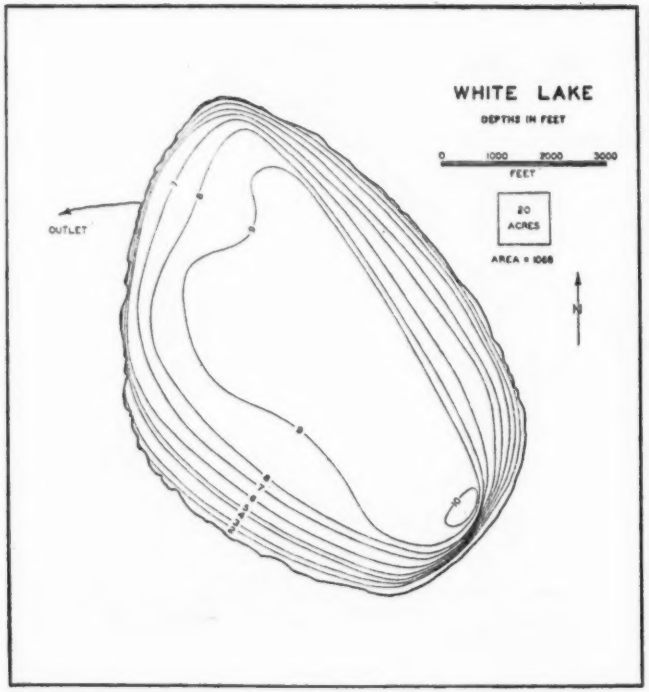


8b

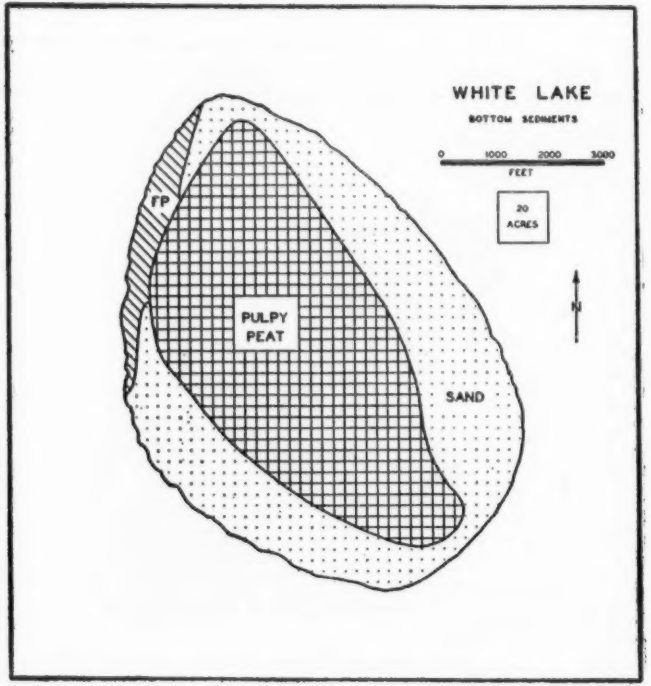


8a

FIG. 8a and 8b. SINGLETARY LAKE. Hydrographic chart and distribution of bottom sediments.



9a



9b

FIG. 9a and 9b. WHITE LAKE. Hydrographic chart and distribution of bottom sediments.

TABLE 12

BLACK LAKE

Bladen County, N. C. 34°40'N, 78°25'W.

Area	1418 acres	Maximum length	3720 yd., 2.11 mi.
Volume	12,197,700 yd.³	Length shoreline	10,400 yd., 5.91 mi.
Maximum depth	7.1 ft.	Shoreline development	1.12
Mean depth	5.3 ft.	Volume development	2.24
		Number of soundings	356

DEPTH	AREA		STRATUM	VOLUME	
	Acres	Per cent of total		Yd.³ × 10⁶	Per cent of total
feet			*feet*		
0	1418	100.0	0–2	4.50	36.9
2	1369	96.5	2–3	2.17	17.8
3	1318	93.0	3–4	2.05	16.8
4	1224	86.3	4–5	1.76	14.5
5	970	68.4	5–6	1.31	10.7
6	664	46.8	6–7	0.41	3.3
7	10	0.7	7–7.1	+	0.004
Total				12.20	100.0

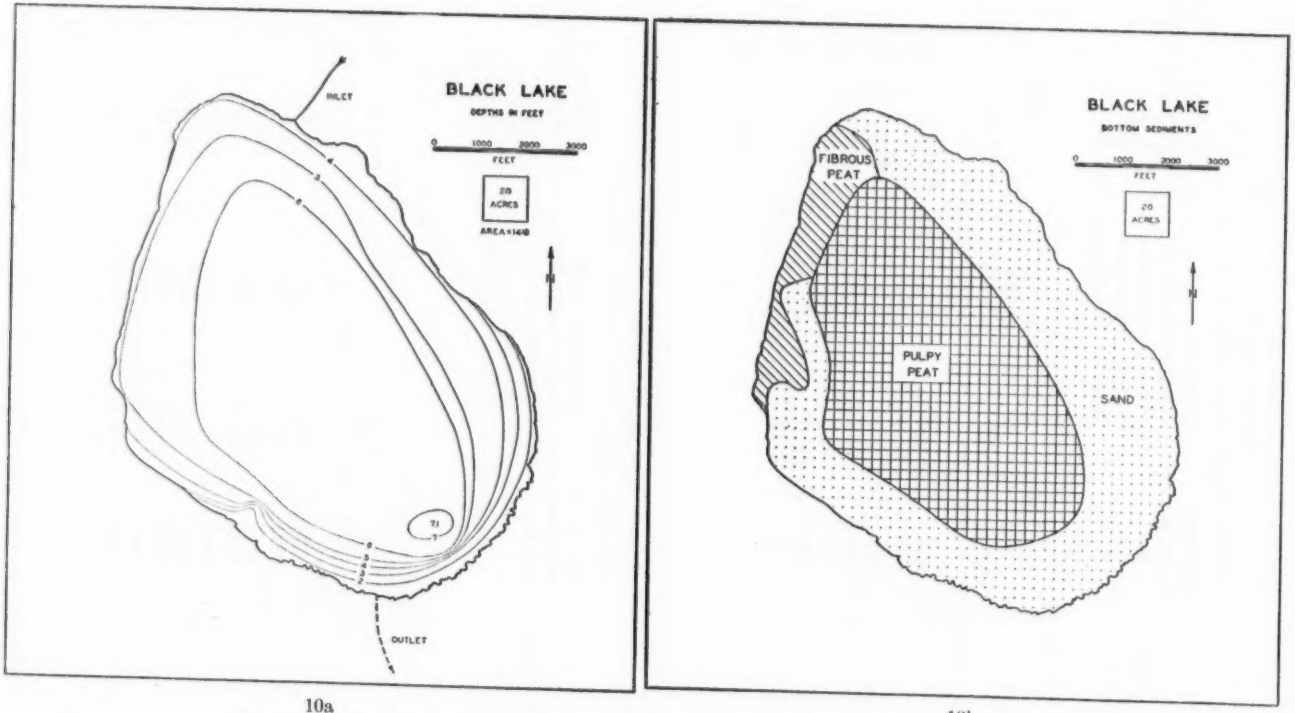
TABLE 13

LAKE WACCAMAW

Columbus County, N. C. 34°17'N, 78°30'W.

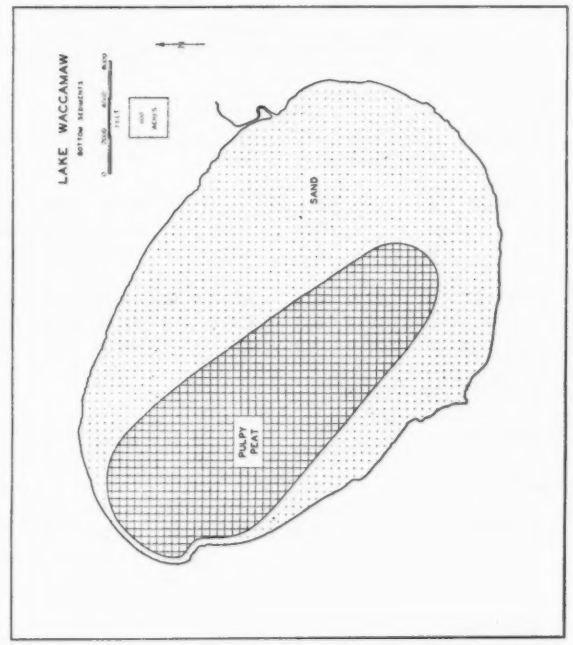
Area	8938 acres	Maximum length	9380 yd., 5.3 mi.
Volume	109,964,800 yd.³	Length shoreline	25,000 yd., 14.21 mi.
Maximum depth	10.8 ft.	Shoreline development	1.07
Mean depth	7.6 ft.	Volume development	2.11
		Number of soundings	502

DEPTH	AREA		STRATUM	VOLUME	
	Acres	Per cent of total		Yd.³ × 10⁶	Per cent of total
feet			*feet*		
0	8938	100.0	0–3	42.25	38.4
3	8523	95.4	3–4	13.17	12.0
4	7804	87.3	4–5	12.15	11.0
5	7264	81.3	5–6	11.25	10.2
6	6684	74.8	6–7	10.46	9.5
7	6289	70.4	7–8	9.79	8.9
8	5850	65.5	8–9	8.75	8.0
9	5002	56.0	9–10	1.41	1.3
10	1705	19.1	10–10.8	0.73	0.7
Total				109.96	100.0

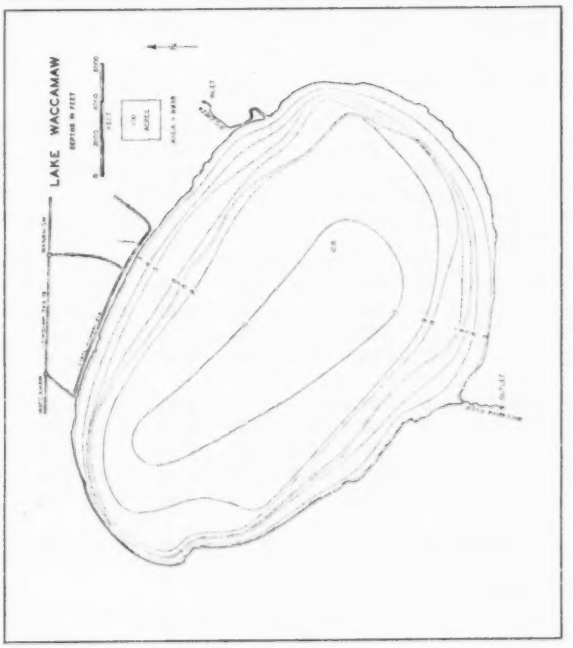


10a 10b

FIG. 10a and 10b. BLACK LAKE. Hydrographic chart and distribution of bottom sediments.



11b



11a

FIG. 11a and 11b. LAKE WACCAMAW. Hydrographic chart and distribution of bottom sediments.

TABLE 14

Chemical and physical observations on the Carolina bay lakes

LAKE	DATE	DEPTH	TEMP.	DISSOLVED O_2		pH	ML. N/44 NaOH PER L.	ML. N/44 H_2SO_4 PER L.	COLOR	DISC
		ft.	°C.	*ppm.*	*per cent*					*ft.*
Jones	13-VI-47	0	28.8	5.7	72		10.93		352	
		6	28.2	5.6	70		11.18	3.19	340	
	17-VI-47	0		6.1			11.13	3.28	340	2.3
		3		5.8			10.83	2.48	340	
		6		5.8			9.13	3.74	340	
	19-VI-47	0	27.9	6.4	81	4.36	11.13	3.15	340	2.1
		3	27.9	5.3	67		11.13	3.96	340	
		6	27.0	4.9	61		11.38	3.11	340	
	24-VI-47	0	24.8							2.3
	31-VIII-47	0				4.31	10.14	2.15	240	2.7
	10-VII-48								260	
Salters	23-VI-47	0	24.1	6.2	72	4.55	13.24	4.00	320	1.8
		3	24.1			4.46	8.83	3.32	352	
		6	24.1	5.9	70	4.44	9.18	3.13	340	
	24-VI-47									1.7
	27-VI-47	0	26.6							2.0
	1-VII-47	0	30.2							1.8
	3-VII-47	0	27.0			4.44	9.68	2.06	280	1.8
		3	27.0			4.51	9.33	2.81	280	
		6	26.8			4.51	9.08	2.69	280	
		8.5	26.7			4.53	9.03	3.13	280	
Singletary	10-VII-47									2.2
	11-VII-47	0	26.4	7.1	87	4.52	6.92	2.19	185	2.3
		3	26.0	7.1	87	4.50	6.92	2.06	180	
		6	25.0	7.0	84	4.51	6.87	2.11	180	
		7.5	24.9	6.9	82	4.53	7.67	2.18	180	
	19-VII-47	0	27.5			4.52	6.86	3.62	170	2.3
		3	27.4	6.4	79	4.55	6.92	2.74	170	
		6	27.3	6.3	77	4.54	6.37	2.56	170	
		9	27.2	6.2	77	4.54	6.32	2.56	170	
		10	27.1	5.9	73	4.51	6.82	2.65	185	
	1-IX-47	0				4.46	6.37	2.35	140	2.9
	4-X-47	0	18.9							2.6

TABLE 14—*Continued*

LAKE	DATE	DEPTH	TEMP.	DISSOLVED O_2		pH	ML. N/44 NaOH PER L.	ML. N/44 H_2SO_4 PER L.	COLOR	DISC
		ft.	°C.	*ppm.*	*per cent*					*ft.*
Singletary *Cont.*	5-X-47	0	19.4							2.9
	16-XI-47								170	
	10-VII-48								160	
White	26-VII-47	0	26.2	6.7	82	4.92	3.26	1.90	12	9
		3	26.2	7.1	86	4.90	3.76	1.85		
		6	26.2	7.1	86	4.95	3.51	1.60		
		7.5	26.2	7.3	88	4.97	3.26	1.69		
	2-VIII-47	0	29.5	6.3	81	4.90	3.71	1.69	<10	9
		3	29.1	6.4	82	4.94	3.36	1.39		
		6	29.0	6.4	82	4.87	3.46	1.43		
		8	29.0	6.5	83	4.91	3.41	1.39	<10	
	10-VII-48								<10	
Black	30-VIII-47	0	27.8	6.3	78	4.43	7.47	2.39	180	1.8
		3	27.5	6.5	80	4.41	7.17	1.98	170	
		6	27.2	6.6	82	4.46	7.47	1.99	175	
	4-IX-47	0	34.9	6.5	92	4.35	7.47	1.60	180	1.8
		1	34.4							
		2	31.0							
		3	29.5	6.6	85	4.38	7.78	1.47	190	
		6	26.6	5.9	72	4.39	7.98	1.68	190	
Waccamaw	15-VIII-47									4.5
	18-VIII-47	0	34.0	5.3	74	7.03	2.66	9.78	140	4.4
		2	30.2							
		3	29.5	5.0	64	6.95	2.66	9.33		
		6	28.6	4.8	61	6.95	3.01	9.28		
		9	28.3	4.6	58	6.92	3.31	9.04	140	
	23-VIII-47	0	30.1	6.1	80	6.91	3.87	8.74	160	4.8
		3	28.8	6.1	77	7.00	4.22	8.53		
		6	28.7	5.8	73	6.93	4.02	8.83		
		9	28.6	5.7	73	6.87	3.92	8.66	170	
	16-XI-47	0	13.2						175	3.8
Big Creek Inlet	23-VIII-47	0	24.0			5.42	24.40	6.89	360	
		0	24.4			5.22	25.45	4.45	400	

LEAF-CURL OF TOBACCO IN VENEZUELA

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INTRODUCTION

The native or criollo varieties of tobacco have long been cultivated in Venezuela although little attention has ever been given to their diseases. In recent years however, certain varieties of the Virginia, Burley, and Turkish types have been introduced there, and have been noted to be affected by several of the common and better-known diseases to which this crop is subject in other tobacco-growing regions of the world. Among the less well-known diseases recently found to occur throughout Venezuela is one known to plant pathologists as leaf-curl or kroepoek. This disease previously has been recorded from the Netherlands East Indies, Africa, and India, where investigations have shown that the causal agent is a virus which is transmitted by white-flies.

Apparently it has not been unequivocally established previously that tobacco leaf-curl occurs in the Americas although a disease tentatively identified as leaf-curl was reported on Burley tobacco in the State of São Paulo, Brazil (Costa and Forster, 1939). There seems little doubt now that the disease investigated in Brazil by Costa (1944) was leaf-curl. He found that the disorder in question was not a "physiological disease", was not transmissible by grafting, and was not caused by arachnids (presumably red spiders), and based his identification of it mainly on this negative evidence. These circumstances appear to warrant the presentation at this time of our findings on tobacco leaf-curl in Venezuela, together with a concise summary of the present status of knowledge of this disease.

HISTORICAL FEATURES

Presumably tobacco leaf-curl was first noted in the Netherlands East Indies, and its incidence there is the basis of an account by Peters and Schwartz (1912).

[1] Employed from October 15, 1947, to May 15, 1948, by the Ministerio de Agricultura y Cría, Departamento de Fitopatología, collaborating with Compañia Anónima Cigarrera Bigott, Sucs., and the Compañia Anónima Venezolana de Tabaco, Caracas, Venezuela. Special thanks are extended to the technicians of these companies for their cooperation, and also to Dr. Clifford H. Meredith, Jefe del Departamento de Fitopatología, for his continued interest and help in this study.

They regarded its cause as unknown. Ludwigs (1913) illustrated and briefly described this disease in the following year, on the basis of his studies in the Cameroons, West Africa. He concluded that tobacco leaf-curl is induced by water relations, noting that a large proportion of the crop was rendered worthless by the disease during the dry season, whereas in the same fields, during the rainy season, a few plants only were affected. He demonstrated that plants adequately supplied with water did not remain free from leaf-curl and he could not apply water in such a way as to induce affected plants to recover.

Thilliard (1921) found no clue to the identity of the infective agent during three years' studies of the disease in the Myombé Plains area of the Cameroons, and was unable to transmit leaf-curl by injecting sap from diseased plants into healthy ones.

Jensen (1920), in an extensive treatise on tobacco diseases in the province of Vorstenland, Java, regarded leaf-curl as of unknown etiology and as among the serious diseases in that region.

The cause of this leaf-curl disease was not established until essentially twenty years after the disorder was first definitely recognized, at which time Storey (1931) at Amani, Tanganyika, and Thung (1932) at Klaten, Java, almost simultaneously announced that it is induced by a virus which is transmitted by a species of white-fly.

A rather extensive series of studies on various phases of the leaf-curl problem has been conducted during the years that have elapsed since its cause was made known from the discoveries by Storey and Thung. These studies deal more specifically with (a) the geographical range of the disease, (b) the entities composing the leaf-curl virus-complex of tobacco and other plants, (c) the primary and alternative hosts and food plants used by the white-fly, and (d) the identity of the vector. Certain pertinent points from these findings may best be considered in the discussions that follow.

RANGE AND IMPORTANCE OF THE DISEASE

In Africa, tobacco leaf-curl has been reported from the Belgian Congo, Cameroons, Gold Coast, Madagascar, Morocco, Nigeria, Nyassaland, Rhodesia, Sierra Leone, Tanganyika, Transvaal, and Zanzibar. It also occurs in such other parts of the Eastern Hemisphere as Java, Sumatra, northern India, Romania, and Russia.

In the Western Hemisphere, as previously stated, it has been reported from Brazil only (Costa, 1944; Costa and Forster, 1939). In Venezuela, tobacco leaf-curl has been observed in the States of Anzóategui, Aragua, Carabobo, Distrito Federal, Guárico, Miranda, Monagras, Portuguesa, and Sucre. Its wide distribution and its wide incidence on criollo tobaccos in remote regions where for several centuries only these native varieties have been cultivated may be interpreted to indicate that the disease has long been present within Venezuela.

It seems agreed that leaf-curl must be regarded as a potentially important disease. The severity of the disorder is stated by Pruthi and Samuel (1942) to be directly correlated with the population of white-fly. These insects are more

abundant in the dry season than in the rainy season, and hence the disease is the more serious in the former period. Storey (1935) regards it as the most destructive tobacco disease in many parts of East Africa. Moore (1933, 1934) noted in East Africa, Rhodesia, and the Transvaal, that half of the crop may be affected in some fields and the entire crop in others. Epiphytotics in southern Rhodesia, in which all the plants were affected, are mentioned by Hopkins (1932). Thilliard (1921) stated that 60 per cent of the crop in the Cameroons was affected in 1917. Costa and Forster (1939) found leaf-curl present to the extent of one to five per cent in Brazil. Pal and Tandon (1937) state that the disorder is usually present in northern India to the extent of five to ten per cent, but that in some fields it virtually destroys the entire crop. In Venezuela, during the dry season, the disease generally involves from five to ten per cent of the crop, although one field of approximately ten hectares was abandoned and plowed up shortly after transplanting because essentially all the plants were affected.

THE DISEASE AND THE VIRUS COMPLEX

Leaf-curl is rarely seen on tobacco in seedbeds in Venezuela although on one hacienda the incidence of affected seedlings in the seedbeds was approximately ten per cent. Infection is usually first noted in the two- to three-week period immediately after transplanting. Young leaves of plants of any age are susceptible, however. Plants affected while young seldom recover and eventually become completely worthless. The uppermost leaves of nearly grown plants may be curled and twisted whereas the older leaves remain normal in appearance (Fig. 3). Occasionally plants are found having curled and twisted leaves in the median stem region although the lowermost and uppermost leaves on such plants may appear normal.

Leaf-curl, the common and generally accepted name of this disorder, fittingly describes one of its most characteristic features (Fig. 1 and 2). Usually too, diseased plants are greatly dwarfed (Fig. 4). Jensen (1920) states that the leaf of an affected plant presents the appearance of having been "kneaded and wrinkled in the hand and again partly unfolded from itself," hence he and plant pathologists in the East Indies have used such names for the disease as "kroepoek," "krupuk," "kroekoh," "kroesblaar," and "krulziekte." The Javanese call it "gilah." English-speaking investigators call it either "leaf-curl," "crinkle", "crinkly dwarf" or "cabbaging". Costa (1944) called it "encarquilhamento do fôlha." The German term "Faltenzwerg", meaning crinkling and dwarfing, is applied to this disease by certain investigators.

Apparently tobacco leaf-curl is not a single disease but a complex of diseases. Thung (1934) described three forms, which he designated common kroepoek, curl or crinkle disease, and transparent kroepoek. In common kroepoek, the leaves are much smaller than normal, their edges curve downward, the smaller veins are knotted and tortuous, and the larger lateral veins bear secondary leaf-like outgrowths or enations. Anatomical studies of such leaf-like structures by Kerling (1933) show that the morphological lower side is directed toward the lower side of the principal leaf. This kind of kroepoek appears to agree with "forma rugosa", as described by Costa.

FIG. 1. Leaf-curl of Virginia tobacco from infection occurring soon after transplanting.
FIG. 2. Leaf-curl involving the bud of a young plant. Such a plant will not produce harvestable leaves.

FIG. 3. Mature leaf-curl-affected plant of Virginia tobacco. Lower leaves are deformed, thickened, and brittle. Plant is branched, with upper leaves severely curled and deformed (Courtesy Ministerio de Agricultura y Cría, Departamento de Genetica.)
FIG. 4. At left, branched plant, without any normal leaves. At right, severely dwarfed plant. (Courtesy Ministerio de Agricultura y Cría, Departamento de Genetica.)

In the curl disease form, the stems are branched (Fig. 4), the margin of the entire leaf is rolled downward, but the midrib and veins are not knotty and crooked. Indefinite-margined yellowish areas usually occur on the oldest leaves that are thick and brittle. This form of leaf-curl is most common in Venezuela. In extreme cases the plants are much dwarfed and the axillary buds continue development to the extent that the plants are broom-like, and apical dominance of the main branch appears quite completely to have been lost. The flower parts, especially the calyx and corolla, are also curled and deformed.

In transparent kroepoek the leaf margins roll upward and the smaller veins tend to become transparent. This form of the disease resembles Costa's (1944) "forma enrolamento."

Pruthi (1937) and Pal and Tandon (1937) recognized five forms of tobacco leaf-curl, designating them A, B, C, D, and X. In forms A and B the plants are markedly stunted, are greener than normal and have leaf-like outgrowths on the larger veins; in A the leaves are smaller, are more curled and thickened, being rugose and brittle, whereas in B they are not thickened and not brittle. The accessory leaf-like outgrowths on the veins are lacking in forms C and D. In both forms the veins are translucent, but in C "stitches" of green occur along the veins. The X form of leaf-curl is a variable complex and appears to be a mixture of all other forms. Pruthi was able to transmit all five types from diseased to healthy plants by means of white-flies, and Pal and Tandon by grafting diseased onto healthy plants.

Kerling (1933), in trying to explain the complex nature of kroepoek, suggested that more than a single virus may be involved and that the white-fly transmits each of them. A further complication arises because some workers regard the cotton leaf-curl virus and the yuca or cassava, *Manihot esculenta* Cranz, leaf-curl virus as identical with the tobacco leaf-curl virus. Holmes (1939), however, regards these as three distinct viruses, a conclusion that is supported by the results to be recounted subsequently of our own reciprocal infection experiments.

THE VECTOR AND TRANSMISSION

The vector of the tobacco leaf-curl virus is known to entomologists generally as *Bemisia tabaci* Gennadius,[2] a member of the family Aleyrodidae. The name *B. gossypiperda*, however, has been widely used instead of *B. tabaci*. The binomial, *B. gossypiperda*, was created in 1929 by Misra and Lamda as a name for the vector of the cotton leaf-curl virus in India.

There now remains the certainty that other genera of aleyrodids and other species of Bemisia may serve as vectors of the tobacco leaf-curl virus, especially in the light of our findings and those by McClean (1940). He stated that *B. tabaci* has not been recorded in the Transvaal and that another aleyrodid, *Trialeurodes natalensis* Cobb, constitutes the leaf-curl virus vector there. In

[2] Gennadius, Agric. ellenica, 1889. Silvestri, in ENTOMOLOGIA APPLICATA GLI INSETTI **1**: 401, 1934, considers *Bemisia gossypiperda* Misra and Lamba (1929) to be synonymous with *B. tabaci* Genn.

Venezuela two species of Aleyrodidae,[3] *Bemisia tuberculata* Bondar and *Aleurotrachelus socialis* Bondar, have been found to be associated with tobacco leaf-curl. Neither species has been observed to breed in large numbers on tobacco, however, but instead mostly on yuca and on several other plant species growing near tobacco seedbeds and fields.

In our preliminary experiments on transmission of tobacco leaf-curl by these aleyrodids, use was made of field-collected insects, mostly from yuca. From ten to approximately one hundred such white-flies were liberated within each of the insect-proof cages, 60 x 60 x 60 cm. in size. Some of the cages covered a group of healthy tobacco seedlings together with one or two leaf-curl-affected plants. Under some of the control cages were placed both diseased and healthy tobacco plants, but without white-flies, and under other controls healthy tobacco plants and white-flies, diseased plants being omitted. Transmission experiments of this sort were made on three haciendas and in the insectary. As a result of enclosing together white-flies, diseased plants, and healthy seedlings under cages, in all locations, thirty-two per cent of the normal plants became leaf-curl-affected. Symptoms were first apparent on some seedlings after 12 days, and 33 days were required for development of the disease in others. All seedlings remained healthy in all cages with both types of controls.

As regards the period of incubation of this disease from other investigations, there is only general accord. Plants are first visibly diseased, as a rule, two to three weeks after viruliferous white-flies are liberated upon healthy plants. Thung (1934) states that the incubation period varies from 22 to 36 days. Undoubtedly a number of factors condition the length of the interval, among them being the age and vigor of the plants or leaves.

Other similar transmission trials involved a field of virus-infected yuca on which white-flies occurred in great abundance. Fifty healthy tobacco seedlings were transplanted on the windward side of this field. Half of these seedlings were immediately screened against white-flies and the others were left unprotected. None of these seedlings, either the protected ones or exposed ones, became affected with leaf-curl. From these results it may be concluded that the virus from yuca is unable to induce leaf-curl in tobacco. Further support for this conclusion stems from observations made in another yuca field which was also abundantly infested with white-flies. On February 24, it was noted that volunteer tobacco seedlings, growing between the rows of yuca, were free from leaf-curl. But on February 26, three leaf-curl-affected tobacco seedlings were transplanted into this field. As a consequence, when on March 9, this field was again visited, one volunteer tobacco seedling had become diseased with leaf-curl. On March 17 there were six additional diseased plants and on March 25, three more were affected. On the other hand, none of the volunteer seedlings became diseased when protected by use of insect-proof cages placed over them at the same time that diseased seedlings were transplanted near-by.

[3] We are grateful to Louise M. Russell, United States Department of Agriculture, Bureau of Entomology and Plant Quarantine, Division of Insect Identification, to whom specimens were sent for identification of these white-flies.

Another test, using this same field, was begun March 18. Thirty tobacco seedlings were transplanted within a short distance of the leaf-curl-affected transplants. Half of them were left exposed to visitation by white-flies and the other half were kept protected under cages. By April 19 eleven of the fifteen seedlings left exposed had contracted leaf-curl whereas all screened plants had remained disease-free. It appears quite certain from these preliminary experiments that either species or both species of white-flies, *Bemisia tuberculata* and *Aleurotrachelus socialis*, are capable of transmitting the virus of tobacco leaf-curl.

There is no evidence to date that insects other than aleyrodids serve as leaf-curl virus vectors. Thung (1932) found that thrips and *Myzus persicae* Sulzer (an aphid) are unable, in Java, to transmit the leaf-curl virus. In Venezuela all the evidence in hand indicates that the suckfly or "mosquito", *Dicyphus minimus* Uhl., is unable to act as a virus vector.

Alternative hosts and food plants which have been reported to exhibit symptoms of leaf-curl after visitation by white-flies are listed below. Many investigators have contributed to this phase of the problem. It has been amply demonstrated that *B. tabaci*, the species that has been assumed generally to be the only vector, uses a wide variety of herbaceous and woody species of plants as food. Many of the plants subsequent to visitation by white-flies, exhibit symptoms of leaf-curl, whereas certain other species remain without symptoms. Moreover, in the light of these studies, it is exceedingly doubtful that a single virus constitutes the etiologic agent for all species that exhibit leaf-curl and that a single species of aleyrodid is the only vector. Many perplexing problems relating to food plants and vectors await solution by use of adequately controlled tests. Whether all the species of weeds and cultivated plants in the following list may properly be regarded as hosts of the tobacco leaf-curl virus has not been established with finality. The list, no doubt, includes hosts for three distinct viruses all transmitted by the same kinds of white-flies, but at this time no one can separate the list into three parts.

Compositae: *Acanthospermum hispidum* D C., *Ageratum conyzoides* L., *Calendula officinalis* L., *Carthamus tinctorius* L., *Cosmos bipinnatus* Cav., *Eupatorium odoratum* L., *Helichrysum monstruosum* Hort., *Inula vestita* Wall., *Launea asplenifolia* Hook., *Synedrella nodiflora* Gaertn., *Vernonia anthelmintica Willd.*, *Vernonia cinerea* Less., *V. hirta* L., *Zinnia elegans* Jacq.

Convolvulaceae: *Ipomoea batatas* Poir.

Cruciferae: *Brassica napus* L., *B. oleracea* L., *B. oleracea* var. *botrytis* L., *B. rapa* L., *Raphanus sativus* L.

Cucurbitaceae: *Cucumis sativus* L., *Lagenaria vulgaris* Ser., *Luffa aegyptica* Mill., L. *acutangula* Roxb., *Trichosanthes anguina* Lam.

Euphorbiaceae: *Euphorbia hirta* L., *Manihot esculenta* Cranz.

Labiatae: *Anisomeles ovata* R. Br.

Leguminosae: *Arachis hypogaea L.*, *Cajanus cajan* Spring., *Cicer arietinum* L., *Crotolaria juncea* L., *Phaseolus calcaratus* Roxb., *Phaseolus mungo* L., *P. radiatus* L., *Glycine hispida* Max.

Linaceae: *Linum usitatissimum* L.
Malvaceae: *Althea rosea* Cav., *Gossypium herbaceum* L., *Hibiscus cannabinus* L., *H. esculentus* L., *H. rosa-sinensis* L., *Sida carpinifolia* L., *S. cordifolia* L., *S. humulis* Cav., *S. rhombifolia* L., *S. veronicaefolia* Lam.
Pedaliaceae: *Sesamum indicum* L.
Scrophulariaceae: *Scoparia dulcis* L.
Solanaceae: *Capsicum annuum* L., *Datura stramonium* L., *Lycopersicum esculentum* Mill., *L. pimpinellifolium* Mill., *Nicandra physaloides* Gaertn., *N. tabacum* L., *N. rustica* L., *N. glutinosa* L., *Petunia violacea Lindl.*, *Physalis angulata* L., *Physalis peruviana* L., *Solanum melongena* L.
Urticaceae: *Cannabis sativa* L.
Verbenaceae: *Stachytarpheta jamaicensis* Gardn.

Thung (1934) concluded that although many species of weeds in Java are used as food plants by *Bemisia tabaci* nevertheless only *Ageratum conyzoides*, *Synedrella nodiflora*, and *Vernonia cinerea* serve as sources of inoculum, and perpetuate the disease when there are no tabacco plants in the fields. Pruthi and Samuel (1942), by means of controlled experiments in which plants were maintained under insect-proof cages, showed that leaf-curl, in India, may be transmitted to tobacco from either *Ageratum conyzoides*, *Crotolaria juncea*, *Euphorbia hirta*, *Launea asplenifolia*, *Lycopersicum esculentum*, *Scoparia dulcis*, *Sida rhombifolia*, *Solanum nigrum*. *Vernonia cinerea*, or *Zinnia elegans*. Van der Lann (1940), by growing tobacco under insect-proof cages in Java, established that *Ageratum conyzoides*, *Eupatorium odoratum*, *Stachytarpheta jamaicensis*, and *Synedrella nodiflora* serve as reservoirs of tobacco leaf-curl virus.

McClean (1940), using diseased tobacco as a source of inoculum, induced leaf curl in *Datura stramonium*, *Helichrysum monstrosum*, *Lycopersicum esculentum*, *L. pimpinellifolium*, *Nicandra physaloides*, *Nicotiana glutinosa*, *Petunia violacea*, *Physalis peruviana*, and *Zinnia elegans*.

Although cotton is included in the foregoing host list, experiments by Storey (1935) showed that leaf-curl is not reciprocally transmissible between cotton and tobacco. Supportive evidence of non-identity of the cotton leaf-curl virus and the tobacco leaf-curl virus is presented by Pruthi and Samuel (1942). They report, for example, that cotton leaf-curl does not occur in some portions of northern India where the tobacco crop is affected, even though white-flies occur on cotton in sufficient numbers seriously to desap the plants.

Evidence remains meagre on the species of plants that serve as reservoirs of virus for the initiation of outbreaks on tobacco in Venezuela. The possibility of survival on tobacco should not be dismissed since at any time of the year there may be living tobacco plants in fields in any of the tobacco-growing regions. In some instances as indicated by our observations tomatoes may function in initiating the disease on tobacco since tomato leaf-curl is widely prevalent in Venezuela. Furthermore when diseased tobacco plants, healthy tomatoes, and white-flies were caged together, the tomatoes in due time became diseased, and when leaf-curled tomatoes, healthy tobacco plants, and white-flies were caged together, the tobacco became leaf-curled. Our results, therefore, support the

experiments involving reciprocal transmission of leaf-curl between tomato and tobacco, recently done in India by Vasudeva and Raj (1948).

SUMMARY

Leaf-curl of tobacco, long known in parts of the Eastern Hemisphere, is widely prevalent in Venezuela.

The diagnostic features of this disorder are curling, twisting and deformation of leaves together with a dwarfing of the plants. This disease is caused by a *virus* that is transmitted by white-flies. The vector in most of the Eastern Hemisphere has been identified as the aleyrodid *Bemisia tabaci*. In the Transvaal it has been identified as *Trialeurodes natalensis* and in Venezuela both *Bemisia tuberculata* and *Aleurotrachelus socialis*, also aleyrodids, may act as vectors.

Many species of plants, as listed herein from previous publications, after having been fed upon by viruliferous white-flies, develop leaf-curl.

It is highly probable that at least three distinct viruses are involved in this leaf-curl complex namely tobacco leaf curl virus, cotton leaf-curl virus, and yuca leaf-curl virus.

Various weeds serve as reservoirs of virus between successive crops of tobacco in the Eastern Hemisphere. Meagre evidence indicates that tobacco and tomato plants act in this capacity in Venezuela.

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THE REDESCRIPTION OF TWENTY-ONE SPECIES OF AREOPIDAE DESCRIBED IN 1923

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Plates 1–4 and One Text Figure

In 1923 the author published a "Key to the Fulgoridae of Eastern North America" (Jour. Elisha Mitchell Sci. Soc. **38**: 139–230, pls. 38–70) in which he described twenty-one new species of the Family Areopidae. At that time not so much attention was being paid to the details of the male genitalia as is now required for the specific determination of species of this family, hence it has been deemed best to redescribe these species from the types.

In order to understand clearly the terminology used in describing the male genitalia of this family, a generalized drawing of the male genitalia of the group is attached. (Text fig. 1). The male genitalia of the Areopidae consists of the modified ninth, tenth, and eleventh abdominal segments. The ninth abdominal segment usually consists of a greatly swollen, somewhat spherical element called the pygofer. The ninth segment is open caudad. This opening is known as the genital opening. The genital opening is usually divided into two areas: the more dorsal, anal region, surrounding the anal segment (tenth segment) and the anal spine (eleventh segment); and the ventral area or genital region. The genital region is divided into an inner compartment and outer compartment by the diaphragm. The anal angle which is usually more or less prominent separates the anal region from the genital region. The aedeagus and its connectives are in the inner compartment and the genital styles are in the outer compartment. The connectives between the aedeagus and genital styles are composed of a basal connective and a pair of aedeagal struts which have a characteristic shape that is of importance in identifying the species. The ventral area of the genital opening is sometimes distinctly separated from the lateral margins by the ventral angles, and in some genera a pair of distinct plates are formed on the ventral border. These may be known as genital plates. In other genera the ventral area may be distinctly separated from the lateral margins of the pygofer which are usually distinctly swollen. This structure may be known as the ventral plate. The genital styles are sometimes simple, flattened, plate-like structures. They may, however, be very elaborate structures with a basal angle strongly developed or with the apical angles developed into elaborate and sometimes branched structures. The aedeagus is usually simple and tubular, sometimes with rows of spines in various areas, sometimes with distinct dorsal processes usually on basal half or with lateral processes usually on basal area. The dorsal margin of the diaphragm which bounds the inner chamber of

the ninth segment is sometimes modified with distinct plates or spines known as the plates of the genital armature. The tenth segment is usually provided with one, sometimes two, pair of anal spines. These spines are sometimes short, produced as anal lobes, sometimes very long, reaching in certain genera to the lower margin of the genital opening. The eleventh segment, known as the anal style, is usually simple, more or less conical and attenuate toward the apex.

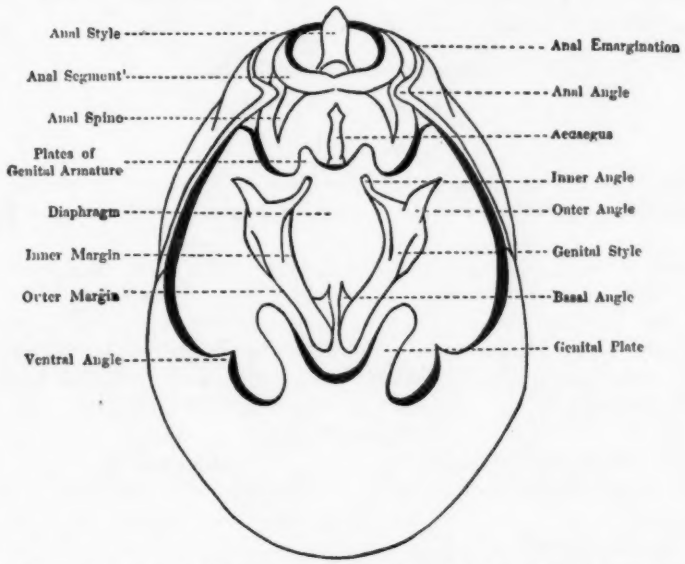


FIG. 1. Generalized view of the caudal aspect of the male genitalia of Areopidae.

Stenocranus arundineus Metc.

(Metcalf 1923a: 197)

(Pl. 1, fig. 5; Pl. 4, fig. 1)

This species may be recognized by its general light orange yellow color without conspicuous black markings except the black eyes and broad short vertex.

Pygofer elongate, narrow. Genital opening elongate, narrow, the outer compartment shallow. Anal angles not produced; ventral angles obtusely produced. Genital styles curving laterad and then gradually attenuate to acute apices which overlap at the tips, exceeding the dorsal margin of the diaphragm. Diaphragm narrow; dorsal margin broadly incised. Anal segment elongate, narrow, somewhat spatulate when viewed dorsad with two pairs of anal spines; the inner pair narrow, gradually acuminate to sharp apices which do not reach the dorsal margin of the diaphragm; outer pair flat, broadened somewhat to the apical third, then suddenly constricted, narrowing to acute apices which are overlapped by the dorsal margin of the diaphragm. Anal style narrow and elongate. Ae-

deagus slender with three apical processes; the dorsal process elongate, recurved at the apex. Aedeagal strut slender, elongate, expanded apically.

Holotype: ♂, Swannanoa, N. C., August 9, 1918. Herbert Osborn and Z. P. Metcalf.

Allotype: ♀, Swannanoa, N. C., August 9, 1918. Herbert Osborn and Z. P. Metcalf.

Paratypes: 10 ♂♂ and 10 ♀♀, collected at Swannanoa, North Carolina, August 1918, from *Arundinaria* sp.

Megamelanus terminalis Metc.

(Metcalf 1923a: 198)

(Pl. 1, fig. 4; Pl. 4, fig. 14)

This species may be recognized by the bicolored wings of the brachypterous male, the strongly spatulate vertex, and the straight lateral carinae of the pronotum.

Pygofer elongate when viewed caudad, longer than wide. Genital opening nearly twice as long as broad. Anal angles obtusely rounded. Diaphragm rather broad; median area distinctly produced, lobe-like. Genital armature with a pair of spine-like processes. Genital styles elongate; outer margin nearly straight; inner margin broadly incised; outer angle broadly rounded; inner angle strongly, acutely produced; genital styles meeting at their apices on the median line. Aedeagus tubular, broadly obtuse at the apex. Anal segment very short; two pairs of anal spines; dorsal pair very short, little more than the produced ventral angles; ventral pair elongate, slender, extending well below the dorsal margin of the diaphragm. Anal style relatively large. Aedeagal strut rather broad, broadly curved.

Holotype: ♂, Carolina Beach, Wilmington, N. C., June 4, 1920.

Allotype: ♀, Carolina Beach, Wilmington, N. C., June 4, 1920.

Paratypes: 5♂♂, Carolina Beach, Wilmington, N. C., June 4, 1920; 4♂♂, Cape Charles, Virginia, July 31, 1920, D. M. DeLong; 10♀♀, Carolina Beach, North Carolina, June 1920; 2♀♀, Cape Charles, Virginia, August 1, 1920, D. M. DeLong.

Megamelanus dorsalis Metc.

(Metcalf 1923a: 199)

(Pl. 2, fig. 7; Pl. 4, fig. 8)

This species may be recognized by its yellowish testaceous head and thorax, and blackish wings, and distinct genitalia.

Pygofer when viewed ventrad elongate, narrow; when viewed laterad elongate, nearly oval. Genital opening when viewed caudad broader than long. Genital chamber deep and the anal sinus deep. Anal angles not much produced. Genital styles elongate, club-shaped; outer margin sinuate; inner margin broadly incised toward the apex; inner and outer angles produced. Diaphragm broad, produced into a pair of curved hook-like processes on the median line, broadly

carinate ventrad of these processes. Anal segment short, rather broad, almost concealed by the pygofer with a pair of short, hook-like anal spines. Anal style short and broad, nearly triangular in outline. Aedeagus elongate, obtuse at the apex. Aedeagal strut rather broad and nearly straight.

Holotype: ♂, Atlantic City, New Jersey, August 25. W. J. Gerhardt.

Allotype: ♀, Atlantic City, New Jersey, August 25. W. J. Gerhardt.

Paratype: ♂, Pascagoula, Miss., August 6, 1921. H. L. Dozier.

Megamelanus lautus Metc.

(Metcalf 1923a: 200)

(Pl. 1, fig. 1; Pl. 4, fig. 6)

This species bears a superficial resemblance to *Megamelanus dorsalis* but the vertex is longer, narrower, the wings are more elongate, brownish fuscous, spotted with white, and the genitalia are distinct.

In this species the pygofer is short and broad; when viewed laterad nearly one and one-half times as long as broad; the dorso-lateral angle broadly rounded, not conspicuous; when viewed caudad the length about the same as the width. Outer chamber shallow. Genital styles nearly rectangular, thick, about five times as long as broad. Bases closely approximate, diverging from each other at about 35 degrees; outer apical angle broadly rounded; inner apical angle acutely produced, reaching beyond the dorsal margin of the diaphragm. Diaphragm large; dorsal margin broadly U-shaped; median line slightly elevated; genital armature with a pair of short, plate-like processes slightly deflexed on the ventral apical angle. Anal segment large; caudal angle produced into a narrow lobe-like process. Anal spines elongate, very slender, gently curved; apex rather acute. Anal style short, broad, ovate. Aedeagus short, obtuse at the apex, complex at the base. Aedeagal strut elongate, narrow at base, widened at apex.

Holotype: ♂, Loma, Texas, December 11, 1910. In the collection of the Illinois State Laboratory of Natural History.

Allotype: ♀, Loma, Texas, December 11, 1910.

Paratypes: ♂, Sarita, Texas, December 5, 1911; ♂, Ocean Springs, Miss., August 15, 1921. H. L. Dozier.

Megamelus distinctus Metc.

(Metcalf 1923a: 201)

(Pl. 2, fig. 10; Pl. 3, fig. 6)

This species may be recognized by its pale frons with the black clypeus and distinct genitalia.

Pygofer elongate. Genital plates distinct, consisting of a pair of lateral lobes which are strongly inflated, broadly rounded at the apex and a median pair of flattened plate-like structures which are triangular at the base; apex produced into a tongue-like process. Outer chamber shallow. Genital styles small, almost concealed by the genital plates, somewhat enlarged basad, gradually

narrowed toward the apex with the inner angle produced triangular. Aedeagus very long, reaching almost to the anterior margin of the pygofer when viewed caudad, broadly curved when viewed laterad with a distinct dorsal process which is obtuse apically, arising from the apex of the basal third. Aedeagal strut short, flat, slightly undulate on both margins. Anal segment short. Anal style elongate.

Holotype: ♂, Portland, Conn., July 25, 1920. B. H. Walden.

Megamelus aestus Metc.

(Metcalf 1923a: 202)

(Pl. 2, fig. 5; Pl. 4, fig. 2)

This species may be recognized by its general blackish color with a median pale vitta evident dorsad and distinct genitalia. Face, antennae, legs, and venter except the abdomen, pale yellow.

Pygofer divided into two areas. A broad ventral plate evident with the lateral areas strongly inflated with a pair of median genital plates elongate, nearly parallel-sided to the apex which is somewhat obtuse. Dorsal area not so strongly inflated. Genital styles small, enlarged at the base, constricted at the middle with the apex expanded; inner angle elongate, rather acute; outer angle broadly rounded. Diaphragm projecting dorsad with an elongate U-shaped incision on the median line and bearing two pairs of acute, spine-like processes; the dorsal pair short; ventral pair elongate, apex curved outward. Outer chamber deep. Aedeagus elongate, slender with an elongate lateral process originating near the base and more than half as long as the aedeagus; with numerous spines on the middle third, apical third smooth and spineless. Aedeagal strut nearly straight, parallel-sided. Anal segment greatly flattened, lateral lobes broadly rounded; in dorsal aspect somewhat spatulate, lateral margins expanding somewhat from the base to the broad apical lobes. Anal style elongate, sagittate with a distinct dorsal lobe at the base.

Holotype: ♂, Carolina Beach, N. C., June 7, 1920. Z. P. Metcalf.

Megamelus inflatus Metc.

(Metcalf 1923a: 203)

(Pl. 2, fig. 3; Pl. 4, fig. 13)

This species may be recognized by its almost uniform pale yellow color with the pygofer of the male strongly inflated, ventral plate complex.

Pygofer rather large, broadly inflated. Ventral plate very distinct; quadrate basal area distinctly set off from the pygofer; dorsal margin with a distinct V-shaped median notch and a small but distinct median spine; genital plates strongly produced with a V-shaped median notch at the apex. Genital styles approximate to apical third, then strongly divergent to rounded apical lobes with the inner angle somewhat produced. Diaphragm long with a V-shaped notch on dorsal margin; dorsal margin produced on the median line. Aedeagus long and slender, nearly straight with a distinct tooth on the dorsal margin about

the middle. Aedeagal strut long and slender, distinctly elbowed at the apex. Anal segment elongate without anal spines. Anal angle inconspicuous. Ventral angle concealed by the genital plates.

Holotype: ♂, Mill Neck, New York, June 19. N. Banks. In the collection of the Museum of Comparative Zoology.

Paratype: ♂, Mill Neck, New York, June 19. N. Banks.

This distinct little species has evidently been confused in the past with *Megamelus notulus* but the male genitalia are entirely distinct.

Megamelus uncus Metc.

(Metcalf 1923a: 204)

(Pl. 2, fig. 11; Pl. 3, fig. 2)

This species may be recognized by its general pale yellow color with the lateral borders of the abdomen broadly black and distinct male genitalia.

In this species the pygofer is broad, strongly inflated. Genital plates arising from a somewhat quadrate ventral plate at the base, narrow, elongate, and incurved. Outer genital chamber large with the diaphragm high, distinctly produced on median area with an apical V-shaped notch, thus producing a pair of plates which are distinctly curved caudad. Genital styles broad, flat, with the outer angle strongly produced. Aedeagus elongate, slender, decurved at the apex with slender recurved spine near apex of basal half. Aedeagal strut, elongate, narrow, somewhat undulate. Anal segment long with a distinct pair of anal spines which are long and acute. Anal style short, rather broad.

The holotype and allotype of this species were labeled simply Anticosti. The only Anticosti listed in Lippincott's Gazetteer is Anticosti Island in the St. Lawrence Bay. I have since learned, however, that these specimens were collected along Anticosti Creek in the District of Columbia.

Holotype: ♂, Anticosti, D.C., August 29. In the collection of the Museum of Comparative Zoology.

Allotype: ♀, Anticosti, D. C., August 29. In the collection of the Museum of Comparative Zoology.

Megamelus anticostus Metc.

(Metcalf 1923a: 204)

(Pl. 2, fig. 13; Pl. 3, fig. 4)

This species may be recognized by the evident pale dorsal vitta, and it is very close to *Megamelus uncus*, but differs in the details of the genitalia.

Pygofer short and very broad. Ventral area strongly inflated and deeply incised on either side of the genital plates. Genital plates elongate; inner margin incised just before the apex with the inner angle obtusely produced; outer margin nearly straight. Genital chamber deep. Diaphragm high, produced into a broad, nearly quadrate plate on the median line with the plate deeply triangularly incised mediad. Genital styles nearly horizontal, enlarged at the base, reduced to acute points at the apex. Aedeagus long and slender, needle-like,

somewhat curved at the base with an elongate recurved process at the apex of the basal third. Aedeagal strut long and narrow, distinctly sinuate. Anal segment elongate with a pair of distinct anal spines which are curved outward. Anal style short and broad.

The holotype and allotype of this species were labeled simply Anticosti. The only Anticosti listed in Lippincott's Gazetteer is Anticosti Island in the St. Lawrence Bay. I have since learned, however, that these specimens were collected along Anticosti Creek in the District of Columbia.

Holotype: ♂, Anticosti, D. C., August 29.

Allotype: ♀, Anticosti, D. C., August 29.

Pissonotus speciosus Metc.

(Metcalf 1923a: 205)

(Pl. 1, fig. 6; Pl. 3, fig. 3)

This species may be recognized by its small size, bright colors, and distinct genitalia.

Pygofer short, narrow and high. Ventral angles slightly produced. Genital opening large; anal angles inconspicuous. Outer chamber rather deep. Genital styles flat, plate-like, approximate on their bases, diverging at an angle of about 90 degrees, then twisting with the inner apical angle produced, the outer apical angle broadly rounded. Diaphragm fairly high, distinctly produced in an acute triangular plate; anal segment rather large with two broadly flattened anal spines which are broad at the base, suddenly constricted at about the middle and then slightly expanded to the obtuse apex. Anal style short, terete at the base, somewhat flattened and rather acute at the apex. Aedeagus tubular, not very long. Aedeagal strut elongate, slightly obtusely expanded on the dorsal margin near the base.

Holotype: ♂, Wrentham, Mass., June 27, 1920. G. W. Barber.

Paratypes: 2♂♂, Wrentham, Mass., June 27, 1920. G. W. Barber.

Pissonotus fulvus Metc.

(Metcalf 1923a: 206)

(Pl. 2, fig. 1; Pl. 4, fig. 12)

This species may be recognized by its almost uniform ochraceous orange color with only the eyes and tips of the tarsi black.

Pygofer large. Genital region of the genital aperture small, almost completely covered by the median genital plate; anal portion very large; anal emargination broadly carinate. Genital plate very large, consisting of two obtuse lateral lobes and a single median lobe which is broadly oval in outline with the dorsal margin with a broad V-shaped notch. Diaphragm large, broadly curved on the dorsal margin. Anal segment large; anal spines broad and flat, broadly oval at the base, suddenly constricted at the middle and narrowed to the acute apex. Genital styles small. Anal style short and broad, almost circular in outline. Aede-

agus elongate, tubular with two pairs of processes at the apex. Aedeagal strut nearly straight, slender, somewhat enlarged at the base and slightly curved.

Holotype: ♂, Paxton, Illinois, July 30, 1916.

Allotype: ♀, Paxton, Illinois, July 30, 1916.

Paratype: ♂, Metropolis, Illinois, August 19, 1916.

Pissonotus nigridorsum Metc.

(Metcalf 1923a: 206)

(Pl. 1, fig. 7; Pl. 4, fig. 4)

This species may be recognized by its general shining black color with the clypeus and legs bright yellow.

Pygofer elongate, narrow. Genital opening narrow, elongate; anal emargination deep. Outer genital chamber deep. Genital plates slender, blade-like, acute at the edge. Genital styles broad, thin, approximate at the base, divergent at an angle of about 90 degrees; the apices strongly reflexed, cup-like. Diaphragm simple with a deep V-shaped notch on the dorsal margin. Aedeagus when viewed caudad, elongate, slender, decurved, sagittate at the apex; when viewed laterad, rather broad and flat. Anal segment rather short, almost included in the anal emargination, with a pair of horn-like anal spines, which are somewhat bulbous at the base, then terete and acuminate, recurved. Anal style elongate, slender.

Holotype: ♂, Greenburg, Pa., September 18, 1904. M. Wirtner.

Delphacodes shermani Metc.

(*Liburnia shermani* Metcalf 1923a: 207)

(Pl. 1, fig. 8; Pl. 3, fig. 1)

This species is close to *L. campestris* Van Duzee but may be recognized by the entirely distinct genitalia.

Pygofer when viewed ventrad slightly broader than long, nearly quadrate, with a distinct median impression caudad; when viewed caudad almost as broad as high, the genital opening very large; anal angles scarcely produced; ventral angles inconspicuous; anal emargination not very deep. Diaphragm very high with the dorsal margin incised, V-shaped, with the lateral margins slightly sinuate; median area somewhat produced. Outer chamber not very deep. Genital styles broad and somewhat bulbous at the base, stem narrow, apex broad and capitate with both the inner and outer angles strongly produced; outer angle obtuse, inner angle acute. Aedeagus broad and short, obtuse at the apex. Aedeagal strut slender, not very long. Anal segment when viewed dorsad nearly quadrate in outline; when viewed caudad short, terete with the median area somewhat produced and a pair of short triangular anal spines. Anal style short and broad.

Holotype: ♂, Raleigh, N. C., late July. F. Sherman.

Allotype: ♀, Raleigh, N. C., late July. F. Sherman.

Paratypes: 5 ♀♀, Raleigh, N. C., late July. F. Sherman.

Delphacodes campestris Van D.

(Muir and Giffard 1924a: 25)

(*Liburnia unda* Metcalf 1923a: 207)

(Pl. 2, fig. 6; Pl. 4, fig. 7)

This is a pale species quite similar to *Liburnia detecta* Van Duzee but may be recognized by its distinct genitalia.

Pygofer short. Genital opening slightly longer than broad; ventral angle slightly produced; anal angles strongly produced; the lateral margin of the genital opening curving outward between the two angles. Outer chamber shallow. Diaphragm rather broad. Genital armature consisting of two reflexed processes which are lined with minute spines on the outer margin; the two are closely appressed on the median line and give the impression, at low power, of consisting of a single tongue-like process. Genital styles elongate, reaching the dorsal margin of the diaphragm, closely approximate on the inner margin; basal angles slightly but not conspicuously produced; outer margin broadly curved; outer angle obtuse; inner margin curved outward at the base and then curved inward toward the apex; the apical angle rather conspicuous. Ventral sinus shallow. Aedeagus compressed, broad at the base, narrow at the apex and produced into a conspicuous dorsal process, usually with a row of minute spines along the dorsal margin at the base. Aedeagal strut compressed, nearly linear in outline with the dorsal apical margin somewhat produced. Anal segment short, nearly concealed by the strongly produced margins of the anal emargination. Anal style elongate, narrow, slightly sagittate.

When I described *Liburnia unda* originally, I had an entirely different species in mind as the *Liburnia campestris* Van D. Muir and Giffard's re-examinations, descriptions, and drawings of the type of *campestris* enable me to make this correction in the synonomy.

Holotype: ♂, Carolina Beach, near Wilmington, N. C., June 6, 1920. Z. P. Metcalf.

Allotype: ♀, Carolina Beach, near Wilmington, N. C., June 6, 1920. Z. P. Metcalf.

Paratype: ♂, Carolina Beach, near Wilmington, N. C., June 6, 1920. Z. P. Metcalf.

Euidella triloba Metc.

(*Liburnia triloba* Metcalf 1923a: 208)

(Pl. 2, fig. 2; Pl. 3, fig. 5)

This species may be recognized by its dull ochraceous brown color, large size, and distinct genitalia.

Pygofer small. Genital region of the genital opening very large; anal region broad and short; anal angle conspicuously produced, elongate, triangular, obtuse at the apex; outer chamber deep. Genital styles complex; bases approximate, shaft curved caudad, then dorsad and terminating in a tri-lobed apical

region with the inner angles overlapping at the apex. Diaphragm not very broad with a broad U-shaped dorsal margin; genital armature complex, consisting of two pairs of spines; a large median pair which curve dorsad, caudad and then ventrad; and a slender lateral pair which curve toward the median line and dorsad to reach the lower margin of the anal segment. Anal segment small without anal spines. Anal style elongate, ovoid. Aedeagus curved, rather broad at the base, narrowed apically and suddenly expanded into two obtuse lobes. Aedeagal strut elongate with a distinct finger-like process at the apex.

Holotype: ♂, New Orleans, La.

Paratypes: 2 ♂♂, Titusville, Fla., November 8, 1911. Cornell University collection.

Delphacodes alexanderi Metc.

(*Liburnia alexanderi* Metcalf 1923a: 209)

(Pl. 2, fig. 4; Pl. 4, fig. 5)

This species may be recognized by the pale yellow color of the head, thorax and legs; the frons, wings and abdomen largely black.

Pygofer rather long. Genital opening large; anal and ventral angles barely indicated. Diaphragm not very high. Outer chamber rather deep. Genital styles conspicuous, approximate on the basal third, then diverging at an angle of about 70 degrees; together somewhat lyre-shaped; outer margin strongly sinuate; outer apical angle acute; inner margin incised on the basal half, the apical half broadly curved to the acute apex. Aedeagus short and blunt, apical area with two rows of small spines, the apical third with a row of stout dorsal spines. Aedeagal strut rather stout, T-shaped. Anal segment small; anal spines close together, somewhat horn-like and rather acute at the incurved apex. Anal style sagittate.

Holotype: ♂, Swannanoa, N. C., August 25, 1919. H. Osborn and Z. P. Metcalf.

Paratypes: ♂, Urbana, Illinois; ♂, Dongola, Illinois, August 21, 1916; ♂, Tupelo, Miss., March 22, 1921, H. L. Dozier; ♂, Falls Church, Va., August 24, N. Banks.

Delphacodes fulvidorsum Metc.

(*Liburnia fulvidorsum* Metcalf 1923a: 210)

(Pl. 2, fig. 9; Pl. 3, fig. 7)

This species may be recognized by the pale yellow color of the frons, vertex, thorax and legs; wings and the abdomen largely black.

Pygofer short and broad. Anal angle produced. Outer chamber shallow. Genital styles rather broad, short; outer margin nearly straight; inner margin broadly incised; apical margin nearly truncate; inner angle slightly produced; outer angle broadly produced, when viewed laterad distinctly sock-shaped. Diaphragm short, incised on the dorsal margin with an obtuse median carina below the incision; genital armature consisting of a pair of closely approximate

short spine-like processes. Aedeagus elongate, tubular with a distinct spine-like process at the base. Aedeagal strut short, L-shaped, basal portion slipper-shaped with an elongate heel. Anal segment short, broad, with a pair of slender anal spines which are curved outward. Anal style elongate, slender.

Holotype: ♂, Brownsville, Texas, December 10, 1910.

Paratypes: 2 ♂♂, Brownsville, Texas, December 10, 1910.

Euidella gerhardi Metc.

(*Liburnia gerhardi* Metcalf 1923a: 210)

(Pl. 1, fig. 2; Pl. 4, fig. 11)

This species may be recognized by its general bright ochraceous yellow color, with the frons narrow, and distinct genitalia.

Pygofer very short and broad. When viewed caudad about as broad as high. Genital opening large; anal angles strongly produced. Outer chamber rather deep; ventral angles not much produced, very obtuse. Genital styles biramose; bases bulbous; inner angle strongly produced, broadly obtuse; outer angle elongate, acute; a distinct, somewhat horn-like process arising from the inner surface just beneath the inner angle. Diaphragm large, broadly V-shaped. Aedeagus short, obtuse at the apex. Anal segment short. Anal spines elongate, reaching the dorsal border of the diaphragm, horn-shaped, curving toward the median line and rather obtuse at the apex. Anal styles short, almost as broad as long, somewhat tongue-like.

Holotype: ♂, Beverly Hills, Ill., August 31, 1907. W. J. Gerhard.

Allotype: ♀, Beverly Hills, Ill., August 31, 1907. W. J. Gerhard.

Paratype: ♀, Chicago, Ill., July 5, 1907.

Delphacodes staminata Metc.

(*Liburnia staminata* Metcalf 1923a: 211)

(Pl. 1, fig. 3; Pl. 4, fig. 10)

This species may be recognized by its pale color, with the frons strongly constricted between eyes, the genital styles slender, the apices suddenly expanded.

Pygofer elongate; when viewed laterad, broadly triangular in outline; when viewed caudad, longer than broad. Genital opening large; anal region especially large; anal angles not produced; ventral angles broadly obtuse, not conspicuous. Diaphragm not very high, produced into a broad median lobe; median line strongly carinate. Genital styles slender, elongate, produced beyond the dorsal margin of the diaphragm; bases approximate; outer margin broadly sinuate; inner margin nearly straight; outer apical angle produced; inner apical angle produced; apical margin broadly produced. Anal segment short; anal spines broad, flat, reaching ventrad beyond the dorsal margin of the diaphragm. Anal style short. Aedeagus simple.

Holotype: ♂, Chicago, Ill., July 25. W. J. Gerhard.

Delphacodes waldeni Metc.

(*Liburnia waldeni* Metcalf 1923a: 212)

(Pl. 2, fig. 12; Pl. 4, fig. 3)

This species may be recognized by its uniform dull brown color and short male pygofer.

Pygofer short and very broad. Genital opening narrow, distinctly widened dorsad; anal angles somewhat produced. Genital styles elongate, rather narrow; bases approximate; basal angle obtusely produced; outer margin broadly incised; inner margin also incised; inner and outer apical angles short, triangular; apical margins produced into an elongate triangular process reaching the anal segment. Outer genital chamber rather deep. Diaphragm not very broad, deeply incised on the thick, dorsal margin. Anal segment broad; anal spines short; anal style short, broad, somewhat sagittate. Aedeagal strut somewhat T-shaped. Aedeagus short, broad, tongue-shaped, obtuse at the apex.

Holotype: ♂, New Haven, Conn., August 8, 1920. B. H. Walden.

Criomorphus conspicuus Metc.

(Metcalf 1923a: 212)

(Pl. 2, fig. 8; Pl. 4, fig. 9)

This species has a general resemblance to *Phyllodinus flabellatus* Ball but the tibiae are terete, not expanded and the median frontal carina is forked on the clypeal margin.

Pygofer short and broad. Genital opening broader than long, almost triangular in outline with a shallow ventral sinus. Outer chamber shallow. Genital styles elongate, nearly horizontal at the base; bases approximate; apex acute, elongate, curved dorsad; outer and inner margins distinctly sinuate. Diaphragm long; dorsal margin produced on median line into a short triangular tube which projects caudad in a triangular process, distinctly carinate on the median line. Anal segment short; anal spines elongate, rather broad at the base, overlapping the dorsal margin of the diaphragm. Anal style short, triangular. Aedeagus short, somewhat expanded at the base and slightly bulbous at the apex which is set with numerous short triangular spines. Aedeagal strut short, somewhat T-shaped, distinctly projecting on the caudal border.

Holotype: ♀, New Haven, Conn., June 1920. B. H. Walden.

Paratypes: ♀, Urbana, Ill., June 1913; ♀, Forest Hills, Mass., August 1919.

DESCRIPTIONS OF PLATES

PLATE 1

Fig. 1. Megamelanus lautus
Fig. 2. Euidella gerhardi
Fig. 3. Delphacodes staminata
Fig. 4. Megamelanus terminalis
Fig. 5. Stenocranus arundineus

Fig. 6. Pissonotus speciosus
Fig. 7. Pissonotus nigridorsum
Fig. 8. Delphacodes shermani

PLATE 2

Fig. 1. Pissonotus fulvus
Fig. 2. Euidella triloba
Fig. 3. Megamelus inflatus
Fig. 4. Delphacodes alexanderi
Fig. 5. Megamelus aestus
Fig. 6. Delphacodes campestris
Fig. 7. Megamelanus dorsalis
Fig. 8. Criomorphus conspicuus
Fig. 9. Delphacodes fulvidorsum
Fig. 10. Megamelus distinctus
Fig. 11. Megamelus uncus
Fig. 12. Delphacodes waldeni
Fig. 13. Megamelus anticostus

PLATE 3

Fig. 1. Delphacodes shermani
Fig. 2. Megamelus uncus
Fig. 3. Pissonotus speciosus
Fig. 4. Megamelus anticostus
Fig. 5. Euidella triloba
Fig. 6. Megamelus distinctus
Fig. 7. Delphacodes fulvidorsum

PLATE 4

Fig. 1. Stenocranus arundineus
Fig. 2. Megamelus aestus
Fig. 3. Delphacodes waldeni
Fig. 4. Pissonotus nigridorsum
Fig. 5. Delphacodes alexanderi
Fig. 6. Megamelanus lautus
Fig. 7. Delphacodes campestris
Fig. 8. Megamelanus dorsalis
Fig. 9. Criomorphus conspicuus
Fig. 10. Delphacodes staminata
Fig. 11. Euidella gerhardi
Fig. 12. Pissonotus fulvus
Fig. 13. Megamelus inflatus
Fig. 14. Megamelanus terminalis

PLATE 1

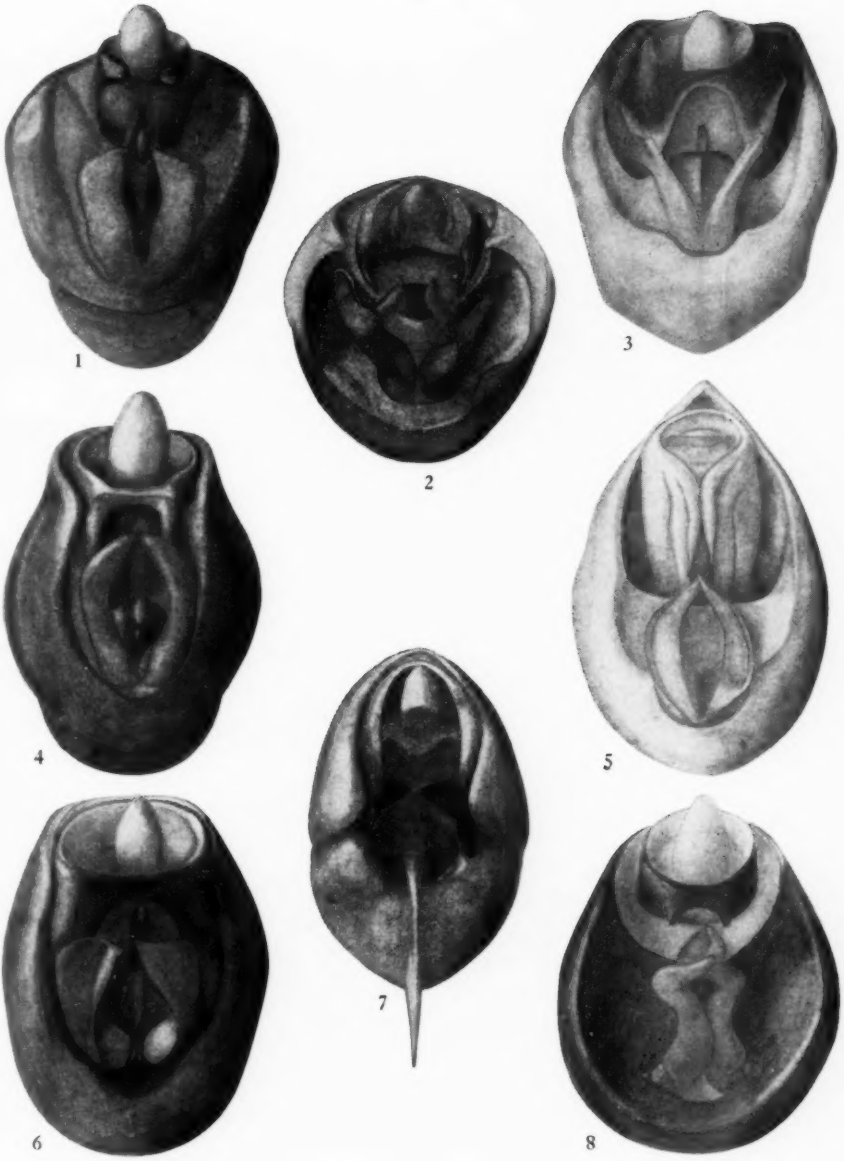


PLATE 2

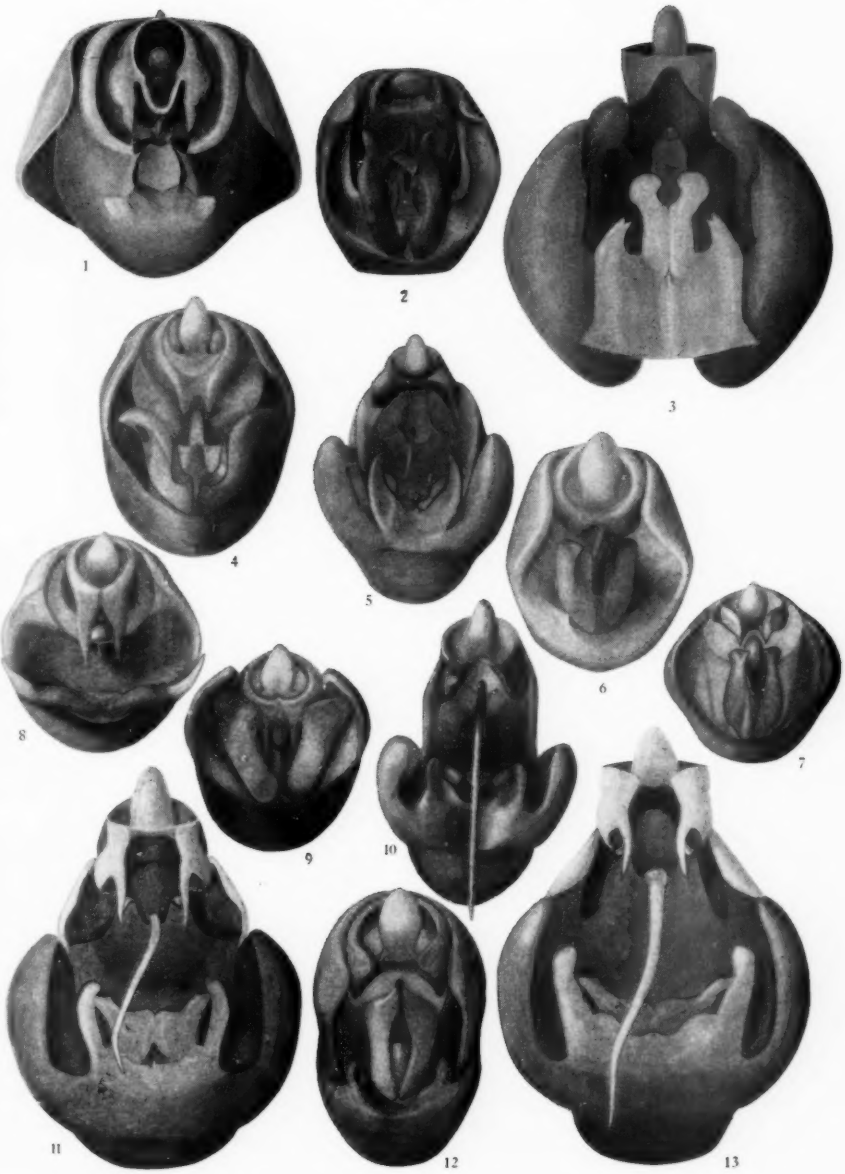


PLATE 3

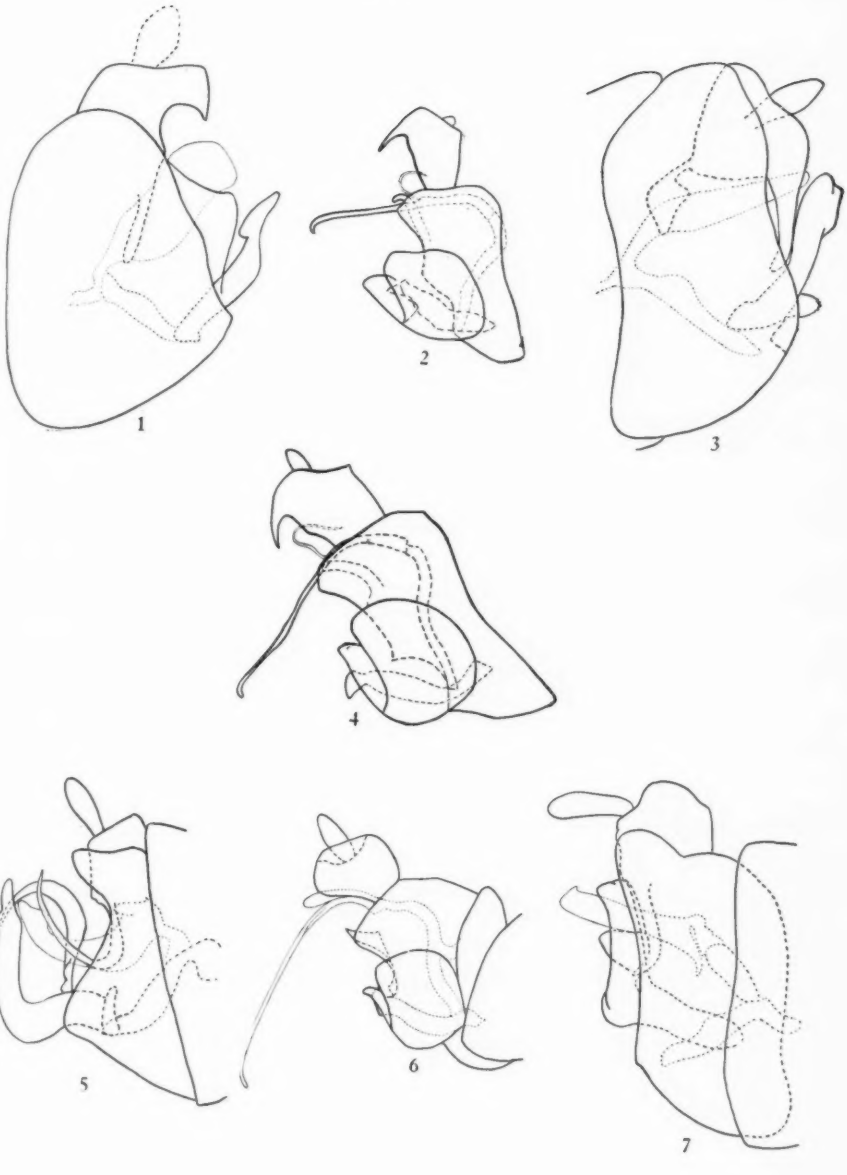
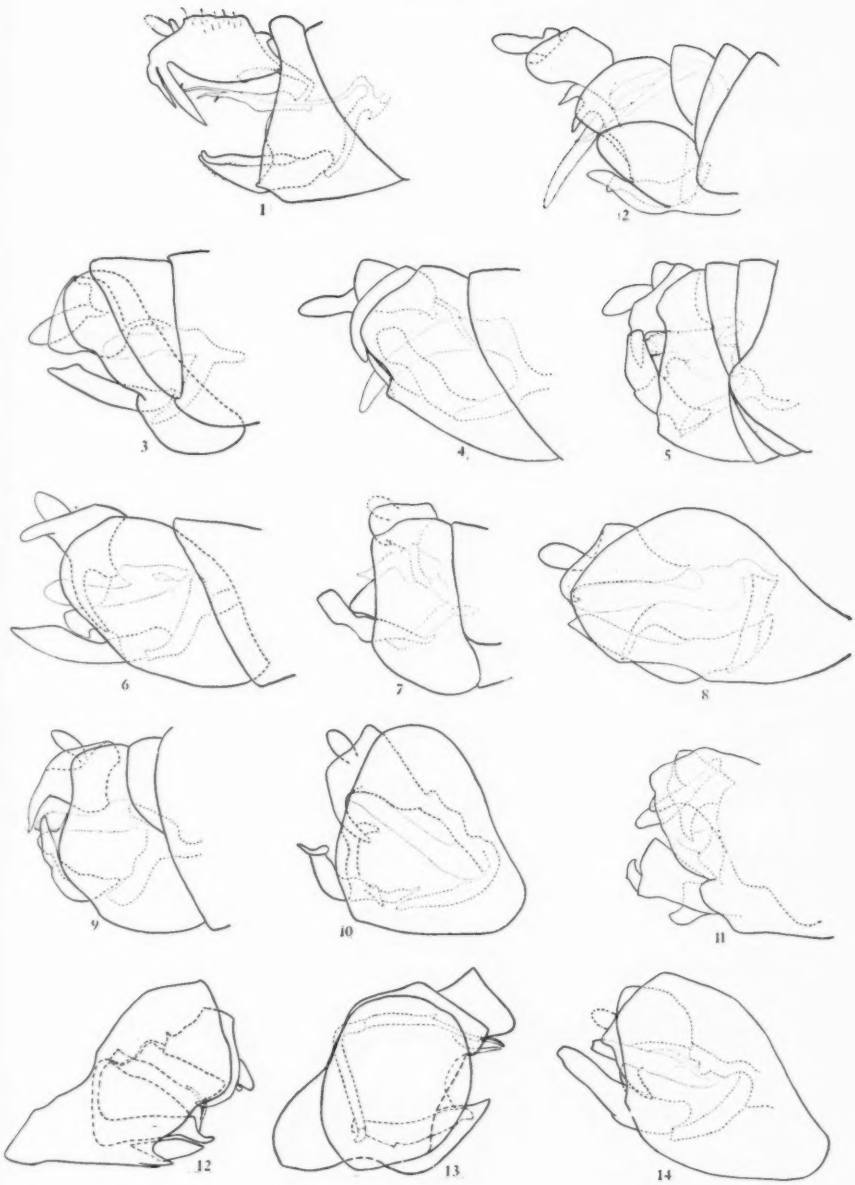


PLATE 4



THE RELATION OF THE MIDGUT TO GROWTH AND DEVELOPMENT OF HABROBRACON, WITH A PERTINENT NOTE ON SPOROZOAN INFECTION

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Plate 5 and 3 Text Figures

In a report of growth in the ecto-parasitic wasp known in genetic literature as *Habrobracon juglandis* (Ashmead) (see Martin, 1947) it was indicated that there are unique features of size increase in parasitic hymenopterous larvae (Grosch, 1948b). Chief among these is the expansible pouch-like midgut which occupies a strikingly large percentage of the larval volume. The present report supplies a summary of specific data in support of this statement and includes observations on mortality due to a sporozoan infection which may indicate the source of reserve materials used in metamorphosis.

MATERIALS AND METHODS

The eugenic wild type stock used in this investigation was reared in an incubator held at 28°C. Larvae of known age were obtained from eggs laid by females during the one-hour periods they were allowed to parasitize a given group of host caterpillars—the larvae of *Ephestia kuehniella* (Zeller). At a desired age (based on Grosch, 1948b) *Habrobracon* larvae were removed from the host, measured, and either dissected for immediate examination or fixed in Bouin's fixative for subsequent study.

Dissections to free the midgut were made in a drop of isosmotic insect Ringer's solution upon a microscope slide. When free in the Ringer's the midguts were measured using an optical micrometer.

Permanent slides were prepared from the fixed larvae by the paraffin method. Serial sections obtained were stained by Heidenhain's iron-hematoxylin method. These were studied under a compound microscope equipped with an ocular micrometer. In addition to furnishing the present results, the slides were useful in a study on the cytological aspects of larval growth (in press).

OBSERVATIONS AND RESULTS

Internal morphology of larvae

In the present paper there are illustrations which should serve in orientation on the morphology of *Habrobracon* larvae. A scale diagram of a lateral view of a mature larva is given in figure 1 and plate 5 presents photographs of longitudinal sections of mature larvae. In addition, the published figure depicting a typical cross section of a mature larva may be consulted (Grosch, 1948b). As

shown in all representations, the most evident larval structure is the large midgut. This structure has only one opening, the valvelike inlet (Fig. 1, V) from the esophagus. The simple tube which is the esophagus leads from the pharynx, a structure with a wall heavily muscled (Fig. 1, M) which enables the pharynx to function as a pumping apparatus. The anterior end of the pharynx extends from the small buccal cavity.

At the posterior extremity of the midgut there is no opening although the anterior end of the hindgut (Fig. 1, HG) is closely proximate. Emptying into the hindgut at this point are the two malpighian tubules (Fig. 1, MT) which extend forward into the thoracic region, lying laterally yet relatively near each side of the ventral nerve cord.

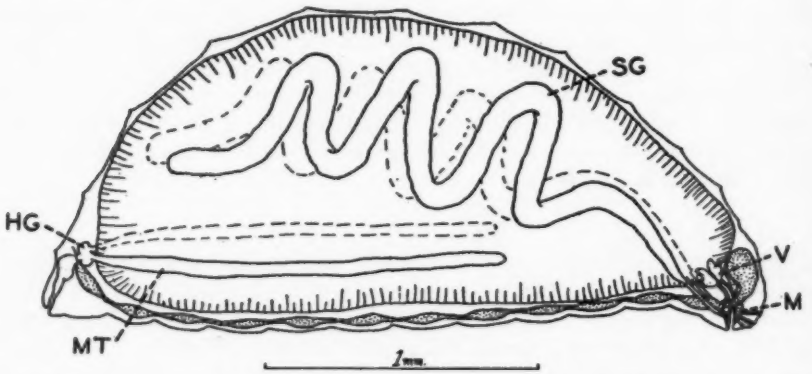

FIG. 1. Diagrammatic lateral view of the mature larval body plan in *Habrobracon juglandis*. Except for size relations this general plan also applies to younger larvae. The limits of the midgut are accentuated by short perpendicular lines. The elements of the central nervous system are stippled. Labels designate other important features as follows: HG = blind end of hindgut, MT = malpighian tubule, M = muscles of the wall of the pharynx, SG = spinning gland, V = valvelike inlet to midgut. Further description is given in the text.

Another pair of tubular structures found between gut wall and body wall are the spinning glands (Fig. 1, SG). These originate ventrally in the head region from a single tube which opens to the exterior by a fine canal on the upper border of the labium. They follow an undulating course laterally down the larva about as far as the posterior limits of the midgut.

The central nervous system is composed of a typically arthropod chain of ganglia which in cross section are seen to be a double arrangement of bilaterally symmetrical parts. These ganglia comprise the supra-esophageal brain and the ventral elements of the nerve cord (stippled in Fig. 1). The space between gut wall and body wall not occupied by tubular or nervous structures is packed with cells of the fat body, fine muscle fibers, and delicate tissues of the respiratory and circulatory systems. The fat cells are the most evident. The impression

of packing is gained from the fact that unlike most insect larvae the fat cells are arranged in only a single layer.

Enclosing and restricting the whole is the body wall, a layer of external cuticula backed by a single layer of epidermal cells except at locations of cellular masses which represent the anlagen of adult appendages.

Relative size of the midgut

Comparison and correlation between the sizes of larvae and of their midgut dimensions were made both in fresh dissections and with permanent slides of

TABLE 1

Measurements in millimeters at greatest dimension

LARVAE (BEFORE DISSECTION)		MIDGUTS (AFTER DISSECTION)		NUMBER
Length	Diameter	Length	Diameter	
.50	.18	.50	.15	3
.60	.20	.60	.20	5
.70	.25	.65	.20	10
.70	.30	.70	.30	5
.70	.40	.70	.35	3
1.35	.60	1.25	.50	4
1.35	.65	1.35	.50	5
1.40	.60	1.35	.60	5
1.50	.60	1.45	.60	5
1.55	.60	1.50	.60	5
1.60	.65	1.60	.60	5
1.65	.75	1.65	.75	1
1.70	.75	1.70	.75	3
1.75	.75	1.75	.75	1
1.82	.75	1.80	.75	2
1.85	.75	1.85	.75	1
1.90	.80	1.90	.80	5
2.25	.85	2.25	.85	2
2.30	.85	2.25	.85	1
2.42	.90	2.40	.90	5
2.50	1.00	2.50	1.00	2
2.65	1.05	2.60	1.00	5
2.75	1.10	2.60	1.05	5

sectioned material. Table 1 presents a series of midgut measurements along with comparable dimensions of larvae from which they were removed. The arrangement presented is based on the order of increase in larval size. Groups into which these data fall were determined by the timed selection of larvae and by the fact that with the lens system used the smallest ocular unit was equivalent to 0.05 mm. This type of data demonstrates that when freed of surrounding tissues the midgut approaches and sometimes even attains the dimensions of the larva from which it was removed. It implies that there is some expansion of the midgut when it is freed from the larval body. A direct demonstration of ex-

pansion can be provided by careful dissections of larvae taken just prior to a moult. Then if a slit is made in the epidermis with care not to puncture the midgut, the midgut will bulge out of and even emerge from the opening. In fact occasionally the entire midgut has actually expelled itself from such a slit.

There are no size differences nor are there larval sex characters whereby males can be easily distinguished from females especially in the early half of larval life. However under the conditions of the experiment at least 50% of the offspring should have been female.

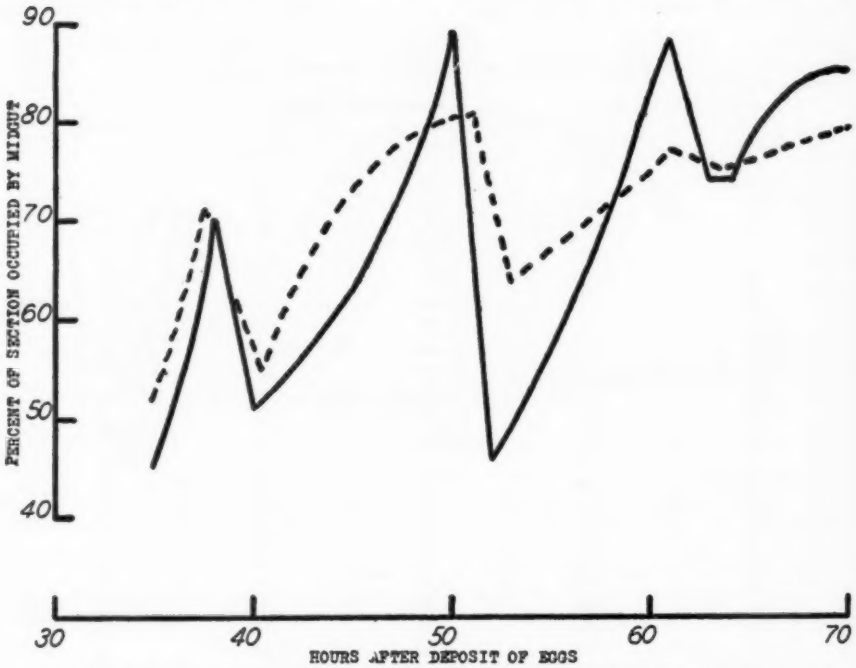

FIG. 2. The percentage of section occupied by the midgut during larval development of haploid Habrobracon. The broken line represents calculations from sagittal sections. The solid line represents calculations from transverse sections of the mid-abdominal region.

Mounted sections provide a basis for making a two-dimensional study of the sectional area occupied by the midgut while in place. After a preliminary survey of slides from larvae of mated females it was decided to restrict study for the time being to a group of offspring in which it would be known that all animals were of the same sex and thus perhaps more homogenous and useful in reference. Such a group of offspring was provided by the parthenogenetically produced males from unfertilized eggs. These offspring from virgin females breed as haploids and are known as haploid males.

A graphic summary of changes which show in sections of haploid larvae are

given in figure 2 by plotting the percentage of the larval section occupied by the midgut against age of the organism. Compared with evidence from transverse sections of 140 larvae, changes in percentage of longitudinal section occupied by the midgut are shown to be more moderate. However the curve with this latter information should be considered with reservation because of the smaller number of longitudinally sectioned larvae (40) on which it is based. Although a complete series is furnished by these longitudinal sections, the critical high points in the curve could have been missed if they are very abrupt in occurrence. Attempts to complete as large a series of longitudinally sectioned larvae as the transverse series were discontinued after a success of less than 40%. Technical difficulties in making longitudinal sections are traceable chiefly to the relatively large midgut.

When these results are compared with "growth" records given by Grosch (1948b) it is found that before each moult the midgut occupies a high percentage of the larval volume; near the beginning of each moult the relative volume occupied by the midgut falls to a low followed soon by an upswing. During the third moult the low percentage occupied by the midgut is not as low as during the two preceding moults. The measurements on which the percentage values are based indicate that it is a change in size of the area occupied by tissues surrounding the midgut which is reflected in the rhythmic curves. The tissue layers appear looser and the individual structural elements seem larger while the midgut shows no more than its usual incremental increase in size. The fact that the amount of actual larval tissue is relatively small by the third moult and cannot contribute much change by its "expansion" is consistent with the failure of relative midgut volume to drop to as low a percentage at the third moult as at other moults.

Increase in larval size which may be due to an "expansion" at the time cuticular restraint is at a minimum has not been distinguishable from the general process of size increase. No sudden changes in size have been observed in studying external dimensions during the period when changes in the ratio of midgut/larva volume are taking place. Imperceptible merging of these with the more general processes undoubtedly complicate the growth curves. Perhaps on this basis may be explained a failure of "breaks" in width curves (later) to correspond with the times of "breaks" in length curves (earlier) (see Grosch, 1948b).

Gut contents and size increase

Examination of fresh preparations discloses that the lumen of the midgut of *Habrobracon* larvae normally contains globules of fat (preferentially stainable with Sudan dyes) and small pieces of host tissue in fluid suspension. When this material is subjected to the solvents used in the paraffin method the fat globules dissolve to leave the fixed suspending fluid as an alveolar artifact (Figure 4). The host tissue fragments, chiefly muscle, do not appear in the midgut contents until the last larval stage unless the host caterpillar is small originally or depleted by the simultaneous feeding of too many other parasites.

Usually, sick host caterpillars can be detected by their appearance and dis-

carded. However in an exceptional case permanent slides were prepared for three *Habrobacon* larvae of a group of five from a diseased host which showed no external signs of illness. Figure 5 presents a photograph of a longitudinal section through one of these larvae. It can be seen that in this case the gut contents are composed chiefly of spores. No organized tissue remnants or alveolar indications of fat globules are visible in the gut lumen. Figure 3 gives an enlarged camera lucida drawing of one of the spores ($13.2 \times 7.2\ \mu$) which shows internal detail. In many other spores, which presumably are more mature, it is difficult to demonstrate the nucleus. Morphologically these spores resemble those of the microsporidian, *Stempellia magna* Kudo (Kudo, 1924) more closely than any of the other species described in available literature. *Stempellia magna* is typically obtained from the fat bodies of various culicine larvae.

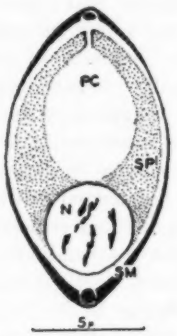

FIG. 3. Camera lucida drawing of a spore with discernible internal structure: N = nucleus, PC = polar capsule, SM = spore wall, SP = sporoplasm.

It is interesting that in spite of their abnormal gut contents the *Habrobracon* larvae showed normal increase in size per unit time. Thus there was no apparent difficulty in the performance of larval functions. The time of spinning and the construction of cocoons seemed normal for the two larvae which were allowed to remain on what is now known to have been a heavily infected host. However, they failed to metamorphose.

DISCUSSION

The internal morphology of *Habrobracon* larvae is very similar to that described for other braconids (refer to the series of papers cited in Grosch, 1948b). A very evident midgut present as a blind sac seems characteristic of all hymenopterous larvae. This type of digestive system has been considered a suitable adaptation to the highly nutritious food hymenopterous larvae normally take or are fed (Carpenter, 1928, p. 183). In the majority of Hymenoptera, however, the midgut occupies only 33% or less of the larval body which is a small volume compared to the values seen in *Habrobracon* larvae. In parasitic Hymenoptera such an extremely large larval midgut seems to be a further adaptation needed

for quick intake and storage of materials which are likely to deteriorate and for which there is competition with other larvae. This was inferred by Seurat as early as 1899. However during intervening years the significance of the large midgut has had little emphasis in spite of frequent descriptions of its presence. Along with the author's 1948b contribution the present report should serve to redirect attention to the importance of the midgut in braconid biology, especially since differences in storage can partially explain the relation between dwarfism and determinate cell size (Grosch, 1948a).

Furthermore, other considerations which extend the importance of the midgut seem indicated. The development of internal pressure reported herewith seems attendant on the forcing of ingested host material into the blind midgut through a one-way valve. In turn, larval increase in size can be related to the intake in the amount of non-living material which is added to the accumulation already in the gut lumen. Substances merely ingested are in actuality not within the physiological interior of the organism, yet, since the lumen of the midgut occupies the significant volume of the larva, it is evident that when one measures larvae at subsequent times in order to make "growth" comparisons, actually it is the amount of non-living—and therefore non-growing—contents added since the last observation which are providing much of the change observed. This of course depends on the pumping action of the foregut and the availability of ingestible materials. Such details seem to explain how *Habrobracon* larvae increase 5 times in length and 7 times in width during less than 40 hours while most other nonparasitic insects take days instead of hours to accomplish comparable increases.

If the normal size and appearance of larvae which ingested chiefly microsporidian spores are considered, it seems evident that only a small fraction of the ingested materials is used to support larval development. Judging from the histological appearance of tissues on serial sections the internal larval structure is entirely normal. There was even no sporozoan invasion of the midgut wall. Nevertheless, death occurred when the two pupated organisms failed properly to undergo metamorphosis. Presumably they differed from equivalent haploids only in their midgut contents—spores instead of fat globules. It seems significant that these two were the only haploid males of this stock which died in the cocoon during the time that the stock was under observation. Such facts along with what is known of metamorphosis in other insects points to a hypothesis that braconids rely on the contents of the midgut rather than on the larval tissues for reserve materials in metamorphosis. As a matter of fact, a mature *Habbrobracon* larva *has* very little larval tissue proper. Except during a moult the living larval tissue comprises strikingly thin layers compressed between midgut and body wall (Fig. 4, Plate 5).

It is not intended that only two specimens be used to justify a generalization. There are situations to which the present is a parallel. These occur in other insects which follow the more common procedure of drawing on the fat body during the histogenesis involved when a holometabolous insect changes to its adult form. Mattes (1928) describes such parallel situations in his discussion of

the pathology of microsporidia in definitive hosts. He indicates that many genera of microsporidia are typically fat body parasites. During larval development, in spite of a great invasion of the fat body, the effect on the outward appearance of infected larvae is small. However the infected larvae cannot develop into normal imagos because the fat body which plays an important role by providing reserves in metamorphosis is not available. It is found therefore that most of the pupae are inviable. Those imagos which do manage to develop from infected larvae show structural abnormalities and are infertile.

Although inferences may be drawn as to what occurs when only a few spores are ingested by a *Habrobracon* larva, the present paper throws no direct light upon the question of the wasp as a vector of sporozoan disease considered in a note by Payne (1933). It is difficult to see how a heavy infection of the present sporozoan can be maintained and transmitted when it results in the death of the potential vector.

SUMMARY

1. The internal morphology of *Habrobracon juglandis* larvae is described.

2. The midgut which is the most evident larval structure is shown by dissection to approach the size of the larva and if observed just prior to a moult, the freed midgut may even expand to the dimensions of the larva which once enclosed it.

3. A study of a series of sectioned haploid male larvae (used to provide a homogenous sample) shows that just before a moult the midgut occupies a very large percentage of the larval volume while during a moult this value falls. This is especially evident during the first two moults.

4. Normally the midgut contents of mature larvae consist of fat globules and a few muscle fragments in liquid suspension. Sectioned larvae from a host (*Ephestia*) infected with a sporozoan parasite showed chiefly spores as the midgut contents. The group had shown normal size increase per unit of time and undisturbed larvae remaining on the same host entered cocoons normally. However they were unable to metamorphose. It seems indicated that braconids rely on a midgut storage of reserves for metamorphosis rather than carry out the more common mode of insect procedure, that of utilizing the fat body.

5. The sporozoan parasite resembles *Stempellia magna* Kudo, a microsporidian usually described from the fat-bodies of culicine larvae.

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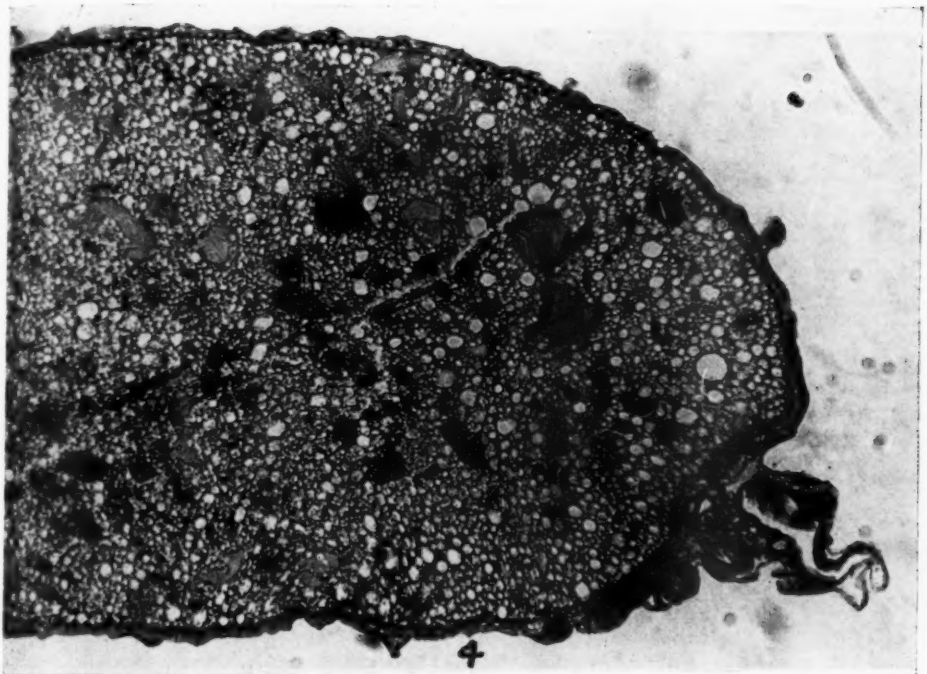
PLATE 5

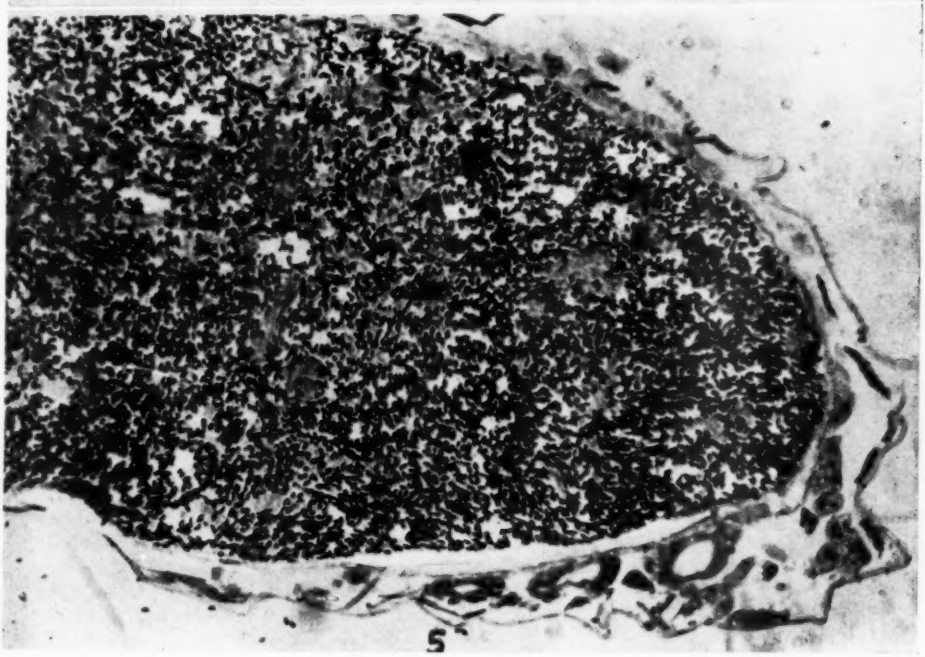
Photographs by Sturgis McKeever (× 80)

FIG. 4. Posterior of a mature Habrobracon larva in sagittal section showing typical large midgut and normal contents of the lumen. Scattered dark areas in the midgut contents are deeply stained muscle fragments.

FIG. 5. Anterior of a mature Habrobracon larva in near-sagittal section showing typical large midgut filled with atypical contents. The dark bodies are microsporidian spores. The spread larval tissue, an aid to cytological examination, is an artifact produced by applying pressure to the cover after mounting.

PLATE 5





THE MYXOPHYCEAE OF NORTH CAROLINA[1]

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Until only recently the Myxophycean Flora of the southeastern states has been very inadequately represented in the literature and herbaria. This was especially true for North Carolina, from which only fourteen species of blue-green algae had been reported prior to 1938. Ravenel in 1877 reported *Scytonema myochrous*; Smith in 1880 reported *Scytonema figuratum* from Warren Springs; Green in 1897 described *Nostoc sphaericum* from Tryon; Stevens in 1908 reported *Porphyrosiphon Notarisii* from Raleigh; and Hoyt in 1917 included ten species of Myxophyceae in his paper on the algae of Beaufort and adjacent areas. In 1938 Drouet checked and published an account of ten specimens collected by Dr. Lewis David von Schweinitz in and around Winston-Salem about 1812.

The first attempt at a systematic study of the Myxophyceae of North Carolina was made by Paul Philson, who published a report on the Cyanophyceae of North and South Carolina in 1939. The results published in this paper were from the findings gathered from a limited number of collections made in a restricted area around Durham. In 1943 L. A. Whitford published an annotated list of "The Fresh-water algae of North Carolina." In this paper he reported all species previously reported from the state, including those listed by Leatherwood in his master thesis at Wake Forest College in 1942. In addition, he added a goodly number of new forms from his own investigation. The total number of species of blue-greens reported by Whitford was one hundred twenty-nine. Blomquist and Humm added nine additional species in 1946, Williams added four more in 1948, and Silva reported one new form. Thus the total number of species which has been recorded to date is 139 (two listed by Leatherwood have been omitted and two others changed because of incorrect identification). Dr. Harold Bold has collected a number of forms in the mountains of North Carolina and Mr. Herman Silva has made limited collections in this area. The author is indebted to Mr. Silva for the records of his and Dr. Bold's collections.

Although this study of the Myxophyceae of North Carolina has been under way since 1939, little was accomplished until 1947. During this time more than two thousand collections extending over most of the state have been made.

The following annotated list includes all species of Myxophyceae which have been reported from North Carolina and, in addition, 136 forms which have not previously been recorded for the state.

[1] The author is grateful for the following research funds which have stimulated and made possible this investigation: grants from the Carnegie Research Fund for the Improvement of Teaching, grants from the A. A. A. S. through the North Carolina Academy of Science, fellowship from the University of North Carolina, and the Margaret Cannon Howell Fellowship from the Highlands Biological Laboratory.

The abbreviations WFC, Wake Forest College; UT, University of Tennessee; and CM, Chicago Museum after the name of a specimen indicates that herbarium specimens are to be found in these places.

CYANOPHYTA

Class **Myxophyceae**

ORDER 1 CHROOCOCCALES

FAMILY 1 *Chroococcaceae*

Chroococcus decorticans A. Braun.
On walls of dams, spillways, and watering troughs. Haywood Co. (Leatherwood), Johnston, Guilford, Warren, Macon, and Jackson Cos. Spring and Summer. WFC #165.

C. dispersus (V. Keissler) Lemmermann.
Plankton. Wayne Co. (Whitford). June.

**C. giganteus* W. West.
Mountains of North Carolina (Bold #95).

C. limneticus Lemmermann.
Widespread and abundant in plankton of small ponds and lakes in Coastal Plain (Whitford). WFC #218. Spring and summer.

**C. macrococcus* (Kuetz.) Rabenhorst.
On dripping rocks, Dry Falls, Macon Co. WFC #273. August.

C. minutus (Kuetz.) Naegeli.
In plankton and mixed with other algae. Wake Co. (Whitford), Lee, Macon Cos. WFC #212. Summer.

C. multicoloratus Wood.
On wooden spillway. Haywood Co. (Leatherwood). August.

C. pallidus Naegeli.
On wet rocks and in old bottles. Wake Co. (Leatherwood), Macon Co. WFC #207. Spring and summer.

**C. refractus* Wood.
Under a dripping spigot at a service station. Carteret Co.

C. turgidus (Kuetz.) Naegeli.
Shallow pools and wet soil. Mountains of N. C. (Bold), Durham Co. (Philson), Coastal Plain (Hoyt, Whitford). WFC #246. Common at all seasons.

**C. Turicensis* (Naeg.) Hansgirg.
On submerged sticks and weeds in lake in city park, Wilmington. New Hanover Co. WFC #247. Summer.

C. varius A. Braun.
Dripping rocks, spillways, and concrete dams. Haywood Co. (Leatherwood), Macon Co. WFC #279. Summer.

* Reported for the first time in North Carolina.

**Gloeocapsa alpicola* (Lyng.) Bornet.
Mountains of N. C. (Silva, CM).

**G. arenaria* (Hassall) Rabenhorst.
Forming scum on flower pots and on wet rocks. Edgecombe and Macon Cos. WFC #302. Summer.

G. conglomerata Kuetzing.
On damp ground in greenhouse, spillways, and dams. Durham Co. (Philson), Wake, Alamance, Caswell Cos. WFC #123.

**G. decorticans* (A. Braun) P. Richter.
On damp soil and bridge footings. Pasquotank, Johnston, Orange, and Wake Cos. WFC #150.

**G. fenestralis* Kuetzing.
On wet boards under the mill at Moore's Mill. Franklin Co. WFC #101. June.

**G. granosa* (Berk.) Kuetzing.
On seeping rocks at Moore's Mill. Franklin Co. WFC #120. June.

**G. magma* (Bréb.) Kuetzing.
Forming a brownish coating on wet rocks. Mountains of N. C. (Bold), Macon Co. WFC #280. August.

**G. nigrescens* Kuetzing.
Mountains of N. C. (Bold #91).

**G. polydermatica* Kuetzing.
On wet beams under dam at the golf course pond, Highlands. Macon Co. WFC #292. August.

G. sparsa Wood.
On dripping rocks. Durham Co. (Philson).

Aphanocapsa delicatissima W. and G. S. West.
Plankton. Lenoir Co. (Whitford). June.

A. elachista W. and G. S. West.
Plankton. Cumberland Co. (Whitford). May.

A. Grevillei (Hassall) Rabenhorst.
Plankton. Durham Co. (Philson), Edgecombe Co. WFC #190. June.

A. pulchra (Kuetz.) Rabenhorst.
In small pools. Bladen and Craven Cos. (Whitford). Spring.

Microcystis aeruginosa Kuetzing.
Common in ponds and pools at all seasons (Whitford). Nash, Wake, Franklin, Dare, Hyde, and New Hanover Cos. WFC #123.

**M. ichthyoblabe* Kuetzing.
Plankton in Wake Forest College Golf Pond. Wake Co. WFC #123. June.

**Anacystis firma* (Kuetz.) Drouet and Dailey.
Mountains of N. C. (Bold).

**A. marginata* Meneghini.
Mountains of N. C. (Bold #156, 158).

**Diplocystis incerta* (Lemm.) Drouet and Dailey.
Mountains of N. C. (Silva).

**Merismopedia aeruginea* Brébisson.
On wet soil. Moore Co. WFC #211. July.

M. elegans A. Braun.
In plankton widely distributed throughout the state (Whitford). WFC #156. Summer.

M. glauca (Ehrenb.) Naegeli.
Wake and Bladen Cos. (Whitford), Washington, Pasquotank Cos. WFC #149, 189. Summer.

M. maior (G. M. Smith) Geitler.
Small pond. Wake Co. (Whitford). February.

M. punctata Meyen.
Small ponds. Bladen and Hyde Cos. (Whitford), Dare Co. WFC #176. May.

M. tenuissima Lemmermann.
Plankton. Wake Co. (Whitford). Spring and fall.

**Holopedium irregulare* Lagerheim.
Mountains of N. C. (Bold #16).

Synechococcus aeruginosus Naegeli.
Among wet mosses where water seeps from hillside. Wake Co. (Whitford). Along edge of fishpond. Cumberland Co. WFC #235. Spring and summer.

**S. Cedrorum* Sauv.
On dripping rocks. Macon and Clay Cos. WFC #272. August.

**S. racemosus* Wolle.
On wet soil in greenhouse at University of North Carolina. Orange Co. WFC #191. June.

**Gloeothece confluens* Naegeli.
On moist earth and in small pools. Wake Co. WFC #233. Summer.

**G. lunata* W. and G. S. West.
In drainage ditch. Pitt Co. WFC #125. June.

G. membranacea (Rabenh.) Bornet.
On wooden spillway. Haywood Co. (Leatherwood). August.

G. rupestris (Lyng.) Bornet.
In ponds among filamentous algae. Carteret and Cumberland Cos. (Whitford). Spring.

**Dactylococcopsis mucicola* Hustedt.
Plankton from millpond near Wilson. Wilson Co. WFC #276. July

**D. rhaphidioides* Hansgirg.
In cooling trough at City Ice Plant, Wake Forest. Wake Co. WFC #116.

**Aphanothece Castagnei* (Bréb.) Rabenhorst.
In pond with *Spirogyra*. Franklin Co. WFC #119. June.

A. conferta Richter.
On dripping rocks. Durham Co. (Philson), Macon Co. WFC #282.
**A. microscopica* Naegeli.
On face of wet rocks. Johnston and Jackson Cos. WFC #304. July and August.
A. pallida (Kuetz.) Rabenhorst.
A wet mass in Duke Greenhouse. Durham Co. (Philson).
**A. saxicola* Naegeli.
Collected in plankton net. Wake and Chowan Cos. WFC #133. June and July.
**A. stagnina* (Sprengel) A. Braun.
On dripping rocks. Mountains of N. C. (Bold); Macon Co. WFC #300. August.
**Coelosphaerium Kuetzingianum* Naegeli.
On submerged rocks in pasture. Stanly Co. WFC #262. July.
C. Naegelianum Unger.
Plankton of ponds and springs. Widespread in Piedmont and Coastal Plain. (Whitford). Spring and fall.
Gomphosphaeria aponia var. *delicatula* Virieux.
From one bog pond. Craven Co. (Whitford). June.
G. lacustris Chodat.
Apparently widespread in the Coastal Plain plankton in spring and summer. (Whitford).

Family 2 *Entophysalidaceae*

Entophysalis granulosa Kuetzing.
On sand on surface of exposed peat above high water, Harker's Island. Carteret Co. (Blomquist, Williams). August.
**E. cornuana* Sauv.
Mountains of N. C. (Recorded by Silva). CM.

Order 2 CHAMAESIPHONALES

Family 1 *Pleurocapsaceae*

Hyella caespitosa Bornet and Flahault.
On oyster shells with *Calothrix crustacea*, Piver's Island. Carteret Co. (Blomquist, Williams). August.

Family 2 *Chamaesiphonaceae*

**Chamaesiphon filamentosus* Ghose.
Mountains of N. C. (Silva #200).
C. incrustans Grunow.
Epiphytic on aquatic mosses and algae. Wake Co. (Whitford, Leatherwood). Winter and spring.

Order 3 HORMOGONALES

Sub-order 1 HOMOCYSTINEAE

Family 1 *Oscillatoriaceae*

Spirulina laxa G. M. Smith.
Small pond. Wake Co., brackish pool. Carteret Co. (Whitford). Winter and spring.

S. major Kuetzing.
In sluggish drain ditch with *Oscillatoria*. Wake Co. (Whitford); along the coast (Williams), Monroe, Union, and Moore Cos. WFC #255. Summer.

S. princeps West and West.
Floating in ponds in Piedmont and Coastal Plain (Whitford). Summer.

S. subsalsa Oersted.
On brackish beach sand and exposed peat. Harker's Island. Carteret Co. (Blomquist). March and August.

**Arthrospira Jenneri* (Kuetz.) Stizenberger.
Collected in plankton net. Washington and Beaufort Cos. WFC #169. June.

**Oscillatoria acuminata* Gomont.
Ponds and sluggish streams. Edgecombe, Johnston, Guilford Cos. WFC #157. June.

O. amoena Gomont.
Slow streams, ponds, and lakes. Haywood Co. (Leatherwood) Lenoir, Wake, and Macon Cos. WFC #290. Summer..

O. amphibia Agardh.
Widespread in small streams and ponds. Wake and Franklin Cos. (Leatherwood). WFC #114. All seasons.

**O. anguina* Bory.
Floating in a small rock pool at Mitchell's Mill. Wake Co. WFC #113. June.

**O. angustissima* W. and G. S. West.
On submerged logs and boards. Pasquotank, Perquimans, and Guilford Cos. WFC #138. June.

**O. brevis* Kuetzing.
Mixed with other algae in tanks at Carolina Biological Supply Co. Guilford Co. WFC #171. Summer.

O. chalybea Mertens.
Scum on a swampy pool. Wake Co. (Whitford). March.

**O. chlorina* Kuetzing.
Along the water edge of a small stream. Lenoir Co. WFC #170.

O. formosa Bory.
Abundant and widespread throughout the Piedmont and Coastal Plain on mud and moist earth (Leatherwood). WFC #106.

O. geminata Meneghini.
Floating. Wake Co. (Leatherwood), Chowan, Camden, Johnston Cos. WFC #134. Summer.

O. lacustris (Kleb.) Geitler.
Shallows of mill pond. Harnett Co. (Whitford).

O. limosa Agardh.
On moist soil. This form was first collected by Dr. Lewis D. von Schweinitz in Forsyth Co. about 1812. Drouet examined von Schweinitz's collections and described them in 1938. Haywood Co. (Leatherwood), McDowell Co. (Philson), Wake, Franklin, and Lincoln Cos. Summer.

O. Meslini Frémy.
Bottom of brook. Wake Co. (Whitford). April.

**O. minnesotensis* Tilden.
On dripping rock below a dam. Chatham Co. July.

O. nigro-viridis Gomont.
"Epiphytic on various algae growing in entangling masses. Perennial but most common in the fall" (Williams).

**O. numidica* Gomont.
In a small pool below a mill pond dam. Wayne Co. WFC #238. July.

O. princeps Vaucher.
Common in sluggish streams and ponds throughout the state (Philson, Leatherwood). WFC #123, 204. All seasons but more abundant in warm weather.

**O. proboscidea* Gomont.
Along the edge of the water in Little River. Pasquotank Co. WFC #150. Summer.

O. prolifica (Grev.) Gomont.
In a wooden spillway. Haywood Co. (Leatherwood). August.

O. sancta (Kuetz.) Gomont.
Abundant in Coastal Plain (Whitford). On flower pots in greenhouse. WFC #166. Summer.

O. splendida Greville.
Common and widespread throughout the state. (Leatherwood). WFC #118. All seasons.

O. subuliformis Gomont.
Attached to New River Lighted Whistle Buoy (Humm). This form is rare in North America. August 21, 1944.

O. subtilissima Kuetzing.
Floating in ponds and slow streams. Wake Co. (Leatherwood), Lee Co. WFC #210. August–October.

O. tenuis Agardh.
Probably the most abundant and widely distributed blue-green in North Carolina. Very common and abundant in slow streams and ponds. (Leatherwood, Whitford, Philson). WFC #126. All seasons.

O. tenuis v. tergestina.
In a small pool, Shackleford Banks. Carteret Co. (Blomquist).

O. Williamsii Drouet.
"On branches of *Pennaria tiarella* (Ayres) 4 ft. below mean low tide level on the protected side of the rocks of the jetty" (Williams). Summer.

Phormidium angustissimum W. and G. S. West.
On the mud bottom of a small stream. Durham Co. (Philson).

P. autumnale (Agardh) Gomont.
"On staircase of barhouse" (von Schweinitz, 1812. Identified by Drouet). Forsyth Co. Widely distributed throughout the state on moist soil and mud (Whitford). WFC #107, 140. Occurs during the entire year but much more abundant in the warmer months.

P. Corium (Agardh) Gomont.
On rocks and mud by small stream. Durham Co. (Philson), Rowan, Mecklenburg, and Union Cos. WFC #206. Summer.

P. crouani Gomont.
In patches on water soaked soil. Durham Co. (Philson).

P. favosum (Bory) Gomont.
Common in standing water (von Schweinitz—1812—identified by Drouet), Durham Co. (Philson), Wake Co. (Leatherwood), Forsyth, Nash, Scotland Cos. WFC #164. Summer.

P. inundatum Kuetzing.
Rare on stones in springs." Forsyth Co. (von Schweinitz, identified by Drouet). Mountains of N. C. (Bold #12).

**P. molle* (Kuetz.) Gomont.
On wet soil. Warren Co. WFC #108. June.

**P. naveanum* Grunow.
Floating at edge of lake. Edgecombe Co. WFC #136. June.

**P. papyraceum* (Agardh) Gomont.
On wet soil by a well in a pig pasture. Rockingham Co. Mountains of N. C. (Bold). CM. WFC #181.

P. Retzii (Agardh) Gomont.
Floating and growing in masses on mud. Forsyth Co. (von Schweinitz, described by Drouet), Franklin Co. (Leatherwood), Durham Co. (Philson). Widespread. WFC #105. Spring, summer, and fall.

P. subfuscum Kuetzing.
On submerged log. Wake Co. (Leatherwood). Spring.

**P. tenue* (Menegh.) Gomont.
In concrete pipe through which water was running. Lee Co. Recorded by Silva from mountains of N. C. WFC #195. July.

**P. tinctorium* Kuetzing.
Mixed with other algae. Guilford Co. WFC #171. June.

P. uncinatum (Agardh) Gomont.
On wet rocks. Forsyth Co. (von Schweinitz, described by Drouet), Wake Co. (Leatherwood, Whitford). Spring.

P. Valderianum (Delp.) Gomont.
On wet rocks. Franklin Co. (Leatherwood). Spring.

Lyngbya aerugineo-caerulea (Kuetz.) Gomont.
Common on mud. Durham Co. (Philson). Widely distributed in Piedmont and Coastal Plain. WFC #111. All the year.

L. aestuarii (Mertens) Liebman.
On mud and moist earth along streams. Durham Co. (Philson).

L. Birgei G. M. Smith.
In a slow stream. Wake Co. (Leatherwood). Spring.

**L. digueti* Gomont.
Edge of watering trough and on flower pots. Mountains of N. C. (Bold); Caswell, Rockingham, Orange Cos. WFC #182. Along the coast (Williams). Spring and summer.

L. ferruginea G. S. West.
Common and widely distributed in stagnant pools. Wake Co. (Leatherwood). Very frequently encountered in Piedmont and Coastal Plain. WFC #104. Entire year.

L. inflexa Frémy.
"Collected once in a decomposing algal mat in early August" along the coast (Williams). August.

**L. Lagerheimii* (Möbius) Gomont.
Abundant in ponds, lakes, and slow streams. Common in all of Piedmont and Coastal Plain. WFC #123. Spring and summer.

**L. lutea* (Agardh) Gomont.
Common on sand along the beach. Dare Co. WFC #151. June.

**L. major* Meneghini.
On damp soil near the river. Mountains of N. C. (Bold), Johnston Co. WFC #162. June.

L. majuscula (Dillwyn) Harvey.
Large mass adrift. Cape Lookout (Humm). September 20, 1941.

L. Martensiana Meneghini.
Submerged rocks and mud. Common in Piedmont and Coastal Plain areas (Whitford, Leatherwood). WFC #102. All the year.

L. nana Tilden.
In an old bottle on the dump, in stagnant pools. Wake Co. (Leatherwood), Wayne, Warren, Halifax Cos. WFC #215.

L. ochracea (Kuetz.) Thuret.
On moist earth and in ponds. Forsyth Co. (von Schweinitz, described by Drouet). WFC #123. Spring and summer.

**L. penicillata* Kuetzing.
On submerged concrete. Rowan and Halifax Cos. WFC #172. July.

**L. putealis* Montagne.
On mud. Caswell Co. WFC #177. June.

**L. semiplena* (C. Agardh) J. Agardh.
On wood exposed at low tide. Dare Co. WFC #143. June.

**L. spirulinoides* Gomont.
On face of concrete dam. Johnston Co. WFC #162. June.

**L. subtilis* W. West.
In a cemetery urn, laboratory jar, and on dripping rocks. Lee, Wake, and Macon Cos. WFC #272. July–August.

Porphyrosiphon Notarisii (Menegh.) Kuetzing.

On moist earth. Forsyth Co. (von Schweinitz, described by Drouet), Wake Co. (Stevens, 1908; Leatherwood). Common in the Piedmont counties. Spring.

Symploca borealis Rabenhorst.

Common on wet soil in early spring. Wake Co. (Leatherwood), Franklin, Granville, Macon, Jackson, Clay, and Chatham Cos. WFC #281. Spring and summer.

**S. dubia* (Naeg.) Gomont.

On moist soil by an old well. Rockingham Co. WFC #185. June.

S. muralis Kuetzing.

On moist soil. Swain Co. (Silva), Hoke Co. WFC #237. Summer.

**S. Muscorum* (Agardh) Gomont.

On moist soil under an outdoor water spigot under shed of an abandoned filling station, Roxboro. Person and Wake Cos. Mountains of N. C. (Bold #343). WFC #179. Summer.

**S. Willei* Gardner.

Base of tree trunks and on moist earth. Wake and Macon Cos. WFC #271. Summer.

**Microcoleus annulatus* F. E. Fritsch.

Forming patches on well packed mud along edge of Lake Asheboro. Randolph Co. WFC #260. July.

M. chthonoplastes (Flora danica) Thuret.

On moist soil both in fresh and brackish conditions. Dare Co. (Hoyt), Wake Co. (Leatherwood), Dare and Currituck Cos. WFC #151. Spring and summer.

M. lacustris (Rabenh.) Farlow.

Common on moist soils and in shallow ponds. Wake Co. (Leatherwood, Whitford). Found in most of the Coastal Plain counties. WFC #110. Common from early spring to late fall.

**M. paludosus* (Kuetz.) Gomont.

On moist soil along Cedar Creek. Jackson Co. WFC #307. August.

**M. sociatus* W. and G. S. West.

On mud and submerged sticks and vegetation. Perquimans, Rowan, Montgomery, and Gaston Cos. WFC #209. Summer.

**M. subtorulosus* (Bréb.) Gomont.

Found growing on concrete footings, moist soils and rocks. Warren and Macon Cos. WFC #285. Summer.

**M. tenerrimus* Gomont.

On soil exposed at low tide. Dare Co. WFC #151. June.

M. vaginatus (Vaucher) Gomont.

Common on wet soil. Widespread throughout the state. (Philson, Leatherwood, and Whitford). WFC #144. Common from early spring to fall.

Hydrocoleum comoides Gom.

"Forming dark-gray patches on rocks about 2 ft. above mean low tide level.

Cape Lookout now becomes the northern limit of its distribution on the east coast of the United States" (Williams). Summer.

**H. homoeotrichum* Kuetzing.

Growing on damp soil in a corn field. Rowan Co. WFC #210. July.

Schizothrix aikenensis (Wolle) Philson.

Mud, decaying vegetable matter in pool. Durham Co. (Philson), Anson Co. WFC #256. July.

**S. arenaria* (Berk.) Gomont.

Clay bank on road east of Highlands Museum. Macon Co. WFC #296. August.

S. Friesii (Agardh) Gomont.

On damp soil and rocks. Durham Co. (Philson), Randolph Co. WFC #253. July.

**S. hyalina* Kuetzing.

On mud along Caraway Creek. Randolph Co. WFC #254. July.

**S. Lamyi* Gomont.

Mountains of N. C. (Bold, CM, UT).

**S. lardacea* (Cesati) Gomont.

Mountains of N. C. (Bold, CM, UT).

**S. Muelleri* Naegeli.

Wet rocks. Mountains of North Carolina (Bold #401), Jackson Co. WFC #270. August.

**S. purpurascens* (Kuetz.) Gomont.

Common on damp soil. Wake, Moore, Nash, Macon, Cabarrus Cos. WFC #213, 275. Summer.

**S. symplocoides* (Gard.) Geitler.

Moist banks. Nash and Macon Cos. WFC #225. Summer.

Forming patches on moist soil along stream. Johnston Co. WFC #160. June.

**S. telephoroides* (Mont.) Gomont.

Moist banks of streams. Johnston Co. WFC #160. June.

**Hypheothrix herbacea* Kuetzing.

Abundant on flower pots in greenhouse. Edgecombe Co. WFC #167. June.

Suborder 2 HETEROCYSTINEAE

Family 1 *Nostocaceae*

Anabaena affinis Lemmermann.

In plankton of ponds. Wayne, Wake Cos. (Whitford), Edgecombe Co. Summer.

A. Azollae Strasburger.

Apparently throughout the Coastal Plain in leaves of *Azolla caroliniana* (Whitford).

**A. confervoides* Reinsch.

On freshwater algae. WFC #264. August.

A. circinalis (Kuetz.) Hansgirg.
"Rare in the plankton of a pool near Princeton, Wayne Co." (Whitford), Bertie Co. WFC #145.

A. Cycadeae J. Reinke.
On roots of a cycad, *Zamia floridana*. Durham Co. (Philson).

A. flos-aquae (Lyng.) Brébisson.
With other algae in small stream in Duke Forest. Durham Co. (Philson).

**A. inaequalis* (Kuetz.) Bornet and Flahault.
In plankton. Wake, Edgecombe, Nash, Martin, Greene, Pitt, Chowan, Johnston, Person Cos. WFC #103. June.

A. laxa (Rabenh.) A. Braun.
On mud in roadside drain. McDowell Co. (Philson), Anson Co. WFC #258. July.

A. oscillarioides Bory.
Forming gelatinous masses in shallow pools. Wake Co. (Whitford), Duplin Co. WFC #230. Summer.

**A. sphaerica* Bornet and Flahault.
Along the edge of Lake Ravenel, Highlands. Macon Co. WFC #299. August.

A. torulosa (Carm.) Lagerheim.
Occurring in plankton. Durham Co. (Philson), Edgecombe Co. WFC #151. June.

**A. variabilis* Kuetzing.
On moist garden soil. WFC #231. July.

**Nostoc comminutum* Kuetzing.
On submerged wood. Pitt and Chowan Cos. WFC #132. June.

N. commune Vaucher.
Widespread on wet soil and seepages. Forsyth Co. (von Schweinitz, described by Drouet). Abundant in Piedmont (Whitford, Curtis). WFC #100. Most abundant in spring and autumn.

N. microscopicum Carmichael.
Common on wet rocks and moist soils. Swain Co. (Whitford), Macon, Jackson, Graham, Orange, and Wake Cos. WFC #193. Summer.

N. muscorum Agardh.
On wet soil. Wake Co. (Leatherwood), Camden, Johnston, Guilford Cos. WFC #147. June.

N. paludosum Kuetzing.
On flooded soil. Durham Co. (Philson), Wake Co. (Leatherwood).

N. parmelioides Kuetzing.
Pools and streams. Wake and Carteret Cos. (Whitford). Spring.

N. peltigerae Letellier.
"The algal symbiont in a lichen common on wet soil." Wake Co. (Whitford). All seasons.

**N. piscinale* Kuetzing.

This is Drouet's annotation on Philson's 1939 herbarium specimen which represented the type of *Anabaena parva* Philson. Wake Co. (Leatherwood). March.

N. punctiforme (Kuetz.) Hariot.

"Forming, with other unicellular species of blue-green algae, a thin coating on submerged rock in a nearby stream." Durham Co. (Philson), Wake, Person, Vance, and Warren Cos. July.

N. sphaericum Vaucher.

On submerged wood. Polk Co. (Green, 1897), Wake Co. (Leatherwood). Spring.

Aphanizomenon flos-aquae (Linn.) Ralfs.

"Occasional in plankton of Coastal Plain ponds" (Whitford); Wilson Co. Summer.

Cylindrospermum alatosporum F. E. Fritsch.

Growing with *Vaucheria*. Durham Co. (Philson).

C. catenatum Ralfs.

On submerged wood. Haywood Co. (Leatherwood), Johnston, Camden, Edgecombe, New Hanover, Duplin, Cleveland Cos. WFC #136. Summer.

**C. comatum* Wood.

On damp soil in greenhouse. Orange Co. WFC #192. July.

**C. licheniforme* (Bory) Kuetzing.

Mountains of N. C. (Bold #380, CM, UT).

**C. majus* Keutzing.

On mud in roadside drain. Mountains of N. C. (Bold #380). WFC #257. July.

**C. minutissimum* Collins.

Muddy banks of Pee Dee River. Montgomery Co. WFC #263. July.

C. minutum Wood.

On *Anthoceros*. Wake Co. (Leatherwood), Caswell Co. WFC #252. June.

C. muscicola Kuetzing.

Along muddy banks. Wake Co. (Leatherwood), Durham Co. (Philson), Alamance Co. WFC #184. Summer.

C. stagnale (Kuetz.) Bornet and Flahault. Mud, damp earth, flower pots. Haywood Co. (Leatherwood), Jackson, Macon, Transylvania, Johnston, and Wake Cos. WFC #162, 293. Summer.

C. trichotospermum Frémy.

Plant masses on mud shaded by large trees. Durham and McDowell Cos. (Philson).

Nodularia Harveyana (Thwaites) Thuret.

In small pools. New Hanover Co. (Whitford), Duplin Co. March, July.

N. spumigena Mertens.

Stagnant pools. Craven Co. (Whitford), Macon Co.

Family 2 *Scytonemataceae*

**Scytonema Arcangelii* Bornet and Flahault.
Attached to rocks and submerged wood. Wake and Wilson Cos. WFC #228.

**S. Austinii* Wood.
On submerged stump in Lake Ravenel, Highlands. Macon Co. Summer.

S. Battersii Gomont.
Wet soil on Ocracoke Island. Dare Co. (Hoyt). August 1918.

S. carolinianum Philson.
Damp rich soil on decaying vegetable matter, decaying grass in road drain. Durham Co. (Philson), Nash Co.

**S. crassum* Naegeli.
Mountains of North Carolina (Bold #302, CM).

S. dubium Wood.
Submerged wood. Macon Co. Summer.

S. figuratum Agardh.
Moist earth and rocks. Warren Springs (Smith, 1880); Buncombe Co. (von Schweinitz 1812, reported by Drouet), Wake Co. (Leatherwood, Whitford).

S. guyanense (Mont.) Bornet and Flahault.
Wet ground and tree trunks. Forsyth Co. (von Schweinitz, 1812, reported by Drouet)

S. Hofmanni Agardh.
Wet wood, rocks and soil. Widespread over the state. (Leatherwood). All seasons.

S. insigne W. and G. S. West.
"Growing in patches on wet soil and limestone rocks." Durham Co. (Philson).

**S. javanicum* (Kuetz.) Bornet.
Moist wood and on base of tree trunks. Warren and Bertie Cos. WFC #178, 129. June.

**S. Millei* Bornet.
On wet rocks and moist soil. Wake and Caswell Cos. WFC #186. Summer.

S. mirabile (Dill.) Bornet.
On moist earth and rocks in streams. Wake Co. (Leatherwood), Pender Co. WFC #253. March–June.

S. myochrous (Dill.) Agardh.
On wet exposed rocks. Reported by Ravenel in 1877. Macon Co. WFC #287. August.

**S. ocellatum* Lyngbye.
With moss at base of tree trunks at water level. Wilson Co. WFC #226. Mountains of N. C. (Bold #374). Summer.

*S. *siculum* Borzi.
On sand and rocks along beach. Dare Co. WFC ⅋153. June.
*S. *varium* Kuetzing.
On submerged wood Lake Asheboro. Randolph Co. WFC ⅋261. July.
*S. *stuposum* (Kuetz.) Bornet.
Forming a brown covering on rocks exposed in river. Johnston Co. WFC ⅋158. Mountains of N. C. (Bold ⅋269).
*S. *tolypotrichoides* Kuetzing.
On submerged boards. Onslow Co. WFC ⅋251. Mountains of N. C. (Bold ⅋147). Summer.
**Plectonema Boryanum* Gomont.
Submerged wood in Wilmington City Park. New Hanover Co. July.
**P. gracillimum* (Zopf) Hansgirg.
Attached to submerged rocks. Macon Co. WFC ⅋267. August.
**P. nostocorum* Bornet.
Seeping rocks. Macon Co. WFC ⅋280. August.
**P. phormidioides* Hansgirg.
On wet rocks with other algae. Dare Co. WFC ⅋152. June.
**P. Tomasiniana* Bornet.
On rocks along edge of Pasquotank River. Pasquotank Co. WFC ⅋155. June.
**Tolypothrix Bouteillei* (Bréb. and Desm.) Lemmermann.
On inner surface of wooden trough just above water level. Rockingham Co.
**T. fragilis* (Gard.) Geitler.
On decaying wood. Warren Co. June.
T. lanata (Desv.) Wartmann.
Shallow pools. Wake Co. (Leatherwood). Widespread in Piedmont and Coastal Plain. Summer.
**T. limbata* Thuret.
On submerged brick. Lee Co. July.
**T. papyracea* Gardner.
On rocks over which water was trickling. Jackson Co. August.
T. penicillata (Agardh) Thuret.
On moist rocks. Wake Co. (Leatherwood). Spring.
T. Rechingeri (Wille) Geitler.
"Growing in a loose mass on trunk of a cedar tree near Duke University." Durham Co. (Philson).
**T. rupestris* Wolle.
On wet rocks at waterfalls. Clay Co. August.
**T. tenuis* Kuetzing.
Attached to wet rocks and submerged boards. Wake Co. (Leatherwood). Apparently occurring throughout the state. Summer.
**Hassalia byssoidea* (Berk.) Hassall.
Mountains of N. C. (Bold).

**Diplocolon Heppii* Naegeli.
On submerged sticks. Onslow Co. WFC #251. July.
**Desmonema Wrangelii* (Agardh) Bornet and Flahault.
On concrete footings in a swift stream. Warren Co. WFC #116. June.
**Microchaete tenera* Thuret.
On wet boards under spillway. Guilford Co. WFC #101. July.
**M. tenuissima* W. and G. S. West.
Attached to the edge of a wooden trough. Craven Co. WFC #185. June.
**Fremyella striatula* (Hy) Drouet.
Mountains of N. C. (Bold #168). Summer.

Family 3 *Stigonemataceae*

Stigonema hormoides (Kuetz.) Bornet and Flahault.
On wet rocks and attached to aquatics. Durham Co. (Philson), Wake Co. (Whitford), Bladen, Wilson, and Macon Cos. WFC #123. All seasons.
S. informe Kuetzing.
Moist and dripping rocks. Durham Co. (Philson), Macon, Wake, and Henderson Cos. WFC #280. Summer.
S. mamillosum (Lyng.) Agardh.
Wet rocks and submerged wood. Wake Co. (Whitford), Wilson, Sampson, Robeson Cos. WFC #229. Summer.
**S. mesentericum* Geitler.
Dripping rocks. Macon Co. WFC #280. Summer.
S. minutum (Agardh) Hassall.
Common on wet soil. Wake Co. (Whitford), Nash Co. WFC #225. All seasons.
S. minutum var. *saxicola* (Naeg.) Bornet and Flahault. On wet rocks. Wake Co. (Leatherwood). March.
**S. mirabile* Beck v. Mannag.
On wet rocks. Macon Co. WFC #284.
S. panniforme Bornet and Flahault.
Dry exposed rocks. Durham Co. (Philson), Macon Co. WFC #295. August.
S. turfaceum Cooke.
Moist earth and rocks. Durham Co. (Philson), Nash, Macon, Cherokee Cos. WFC #266. Summer.
**S. tomentosum* (Kuetz.) Hieronymus.
Exposed rocks. Jackson, Clay, and Macon Cos. WFC #298, 269. August.
Fischerella ambigua (Naeg.) Gomont.
In pools and on submerged rocks and wood. Johnston, Cumberland, Swain Cos. Mountains of N. C. (Bold). WFC #234. Summer.
**F. Letestui* Frémy.
On partially submerged wood. Wayne and Johnston Cos. WFC #161. July.

F. maior Gomont.
On submerged stems and leaves. Pender Co. (Whitford), Wilson Co. WFC #237. July.

**F. muscicola* (Thuret) Gomont.
On moist clay. Wake Co.

**F. thermalis* (Bornet and Flah.) Gomont.
Mountains of North Carolina (Bold #224, CM, UT).

**Hapalosiphon arboreus* West and West.
With moss and other algae on a wet clay bank. Wake Co. WFC #249. Spring and summer.

H. aureus West and West.
Submerged log, moist earth in drain canal. Wake Co. (Leatherwood), Craven Co. July.

**H. flexosus* Borzi.
On submerged roots in White Lake. Bladen Co. WFC #224. July.

H. fontinalis (Agardh) Bornet.
On submerged wood or aquatics. Bladen, Craven, and Wake Cos. (Whitford), Haywood Co. (Leatherwood). WFC #248. Common at all seasons.

H. hibernicus W. and G. S. West.
Growing on submerged wood and vegetation. Wake and Craven Cos. (Whitford), Moore Co. WFC #259. July.

**H. intricatus* West and West.
On wood beams under dam at golf course pond, Highlands. Macon Co. WFC #292. August.

H. Welwitschii W. and G. S. West.
On moist soil. Durham Co. (Philson).

Family 4 *Rivulariaceae*

**Amphithrix janthina* (Mont.) Bornet and Flahault.
On wet concrete under mill near Wilson. Wilson Co. Mountains of N. C. (Bold). WFC #216. July.

**Calothrix adscendens* (Naeg.) Bornet and Flahault.
With other algae in water fountain in Wilmington. New Hanover Co. WFC #245. July.

C. Braunii Bornet and Flahault.
On wet boards, rocks, and dams. Durham Co. (Philson), Haywood Co. (Leatherwood), Wake, Franklin, Sampson, Macon, Jackson, Lincoln, Edgecombe, Nash, Hyde, and Vance Cos. WFC #101. Summer.

C. confervicola C. Agardh.
Epiphytic on sea weeds. Piver's Island (Blomquist); Dare Co. WFC #168. June.

C. crustacea Thuret *in* Bornet and Flahault.
On oyster and clam shells along the beach, Piver's Island (Blomquist, Williams); Atlantica, Carteret Co. June and July.

**C. donelli* (Wolle) De Toni.
Attached to submerged wood. Chowan Co. WFC #132. June.

**C. Elenkinii* Kossinskaja.
On submerged rocks at drinking fountain, Mr. Morrow. Stanly Co. WFC #251. July.

**C. epiphytica* West and West.
On green algae. Camden Co. WFC #137. June.

C. fusca (Kuetz.) Bornet and Flahault.
Mixed with other algae. Wake Co. (Leatherwood), Edgecombe, Bertie, Camden Cos. WFC #124. June.

C. juliana (Menegh.) Bornet and Flahault.
On concrete dam. Haywood Co. (Leatherwood). August.

**C. parietina* (Naeg.) Thuret.
On moist rocks and in water fountain. Jackson, Nash, New Hanover, and Rutherford Cos. WFC #187. Summer.

**C. prolifera* Flahault.
Submerged wood in salt water. Dare Co. WFC #154. June.

**C. pulvinata* Kuetzing.
On stump exposed at low tide, Nag's Head. Dare Co. WFC #148. June.

C. scopularum C. Agardh *ex* Bornet and Flahault.
On buoy mixed with other algae. Cape Lookout Shoal Station Buoy No. 14 (Humm); along the coast (Williams). Summer.

C. scytonemicola Tilden.
Ponds. Wake Co. (Leatherwood). Spring.

**C. simulans* Gardner.
Lake Ravenel, Highlands. Macon Co. WFC #309. August.

**C. stellaris* Bornet and Flahault.
Mountains of N. C. (Bold #173, CM, UT).

**Dichothrix Baueriana* (Grunow) Bornet and Flahault.
On dripping rocks with other algae. Macon Co. WFC #289. August. Mountains of N. C. (Bold #173, CM, UT).

**D. compacta* (Agardh) Bornet and Flahault.
On submerged stump in White Lake. Bladen Co. WFC #223. July.

D. fucicola (Kuetz.) Bornet and Flahault.
Epiphytic on *Sargassum natans*. Harker's Island, Carteret Co. (Blomquist).

**D. gypsophila* (Kuetz.) Bornet and Flahault.
On dripping rocks. Jackson Co. WFC #274. August.

**D. Meneghiniana* (Kuetz.) Forti.
On submerged wood. Cumberland Co. WFC #236. July.

**D. orsiniana* (Kuetz.) Bornet and Flahault.
On submerged rocks and boards. Pasquotank and Jackson Cos. WFC #139. Summer.

**D. spiralis* Fritsch.
A few filaments collected in a shallow rock pool at Mitchell's Mill. Wake Co. WFC #103. June.

**Rivularia Beccariana* (deNot.) Bornet and Flahault. Mountains of N. C. (Bold #165, UT).

Gloeotrichia echinulata (J. E. Smith) P. Richter.

On submerged aquatics or floating. Wake and Wilson Cos. (Whitford), Guilford Co. WFC #172. Summer.

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ADDITIONS TO THE ALGAE OF THE SOUTHEASTERN UNITED STATES

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Until the last two decades there have been but few investigators of the algae among resident botanists of the southeastern United States, and there are still few research facilities for the pursuit of phycological studies in the region, such as herbaria and libraries. During the past twenty years, however, interest in the algae has gained momentum because of the establishment there of a small group of trained investigators who have a special interest in local algal flora.

Whereas development of recreational fishing in the Mid-west stimulated special, intensive phycological work, the studies in the Southeast have remained almost exclusively general, and for the most part systematic. Among the studies, however, have been two special investigations on soil algae which open the door on what should be a most productive field. A résumé of the more significant of the published studies, and a southeastern bibliography of sixty-one titles can be found in Silva (1948).

During the writer's studies extending over the past six years, it has become apparent that an over-all picture of the algal flora of the region would be valuable. In order to relate the many individual reports, some of which are very limited in scope, a catalogue has been prepared in which the algae known for the ten southeastern states are listed. This compilation will be published soon as a contribution toward a general conspectus.

At present, publication of algal studies has lagged rather far behind collection and identification so that valuable records are not generally available. It is the purpose of the present paper to make known some of these records, whereas the catalogue will include all known published reports.

There has been such an accumulation of information that the publication of all of it does not seem practicable and the following course has been adopted:

1. The forthcoming catalogue will include previously published references only, the dates and authors of publications applying to the species being systematically assembled.
2. Original collection data, which have not been published previously, appear here. States are used as the unit area of reporting.
3. The writer's identification of species already reported from a state are not mentioned.
4. When two or more identified collections of a single species were found from a particular state, only one is mentioned.
5. Exceptions to these rules are usually noted in the text.
6. The Cyanophyta are not included herein.

Much of the credit for this paper is due to Dr. H. C. Bold who has provided the

substantial set of specimens and records assembled with the aid of his students in four states, Dr. G. W. Prescott for the opportunity to examine his Florida collections and for his valuable guidance, and to Mr. Hugh H. Iltis and Mr. Albert Clebsch for their cooperation.

The following abbreviations will be found in the text:
B—H. C. Bold
GP—G. W. Prescott
H—H. C. Bold
S—Herman Silva

Phylum CHRYSOPHYTA

Class **Heterokontae**

Order HETEROCOCCALES

Family *Ophiocytiaceae*

Ophiocytium Naegeli 1849

1. *Ophiocytium cochleare* A. Braun—TENN., among filamentous algae in pool near Glen Echo Lake, Davidson Co. Feb. 19, 1939, B-3936.

Order HETEROTRICHALES

Family *Tribonemataceae*

Tribonema Derbes & Solier 1856

1. *Tribonema minus* (Wille) Hazen—S. C., branch in field near Walhalla, Oconee Co. May 21, 1939; FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.
2. *T. utriculosa* (Kuetz.) Hazen—N. C., on grass in spring branch and swamp in running water near Pearson's Lake, Polk Co., with *Draparnaldia* sp. May 5, 1939, H-16.

Order HETEROSIPHONALES

Family *Botrydiaceae*

Botrydium Wallroth 1815

1. *Botrydium granulatum* (L.) Grev.—TENN., moist soil, Orphans' Home, Spring Hill, Maury Co. Sept. 24, 1938, B-132.

Class **Chrysophyceae**

Order CHRYSOMONADALES

Family *Chromulinaceae*

Chrysopyxis Stein 1878

1. *Chrysopyxis* sp.—S. C., on *Mougeotia* sp. in swamp near Cedar Mt. Greenville Co. Aug. 10, 1939, H-432.

Family *Ochromonadaceae*

Dinobryon Ehrenberg 1835

1. *Dinobryon divergens* (Stokes) Lemm.—TENN., Chilowee Park Lake at Knoxville, Knox Co. June 29, 1938, Bold.
2. *D. sertularia* Ehr.—TENN., Chilowee Park Lake at Knoxville, Knox Co. July 15, 1938, Bold.

Uroglenopsis Lemmerman 1899

1. *Uroglenopsis americana* (Calkins) Lemm.—N. C., Phillips Lake, 18°C. Macon Co. May 15, 1939, H-26.

Phylum CHLOROPHYTA

Class **Chlorophyceae**

Order VOLVOCALES

Family *Chlamydomonadaceae*

Carteria Diezing 1886

1. *Carteria Fritschii* Takeda—N. C., Phillips Lake, temp. 18°C, Macon Co. May 11, 1939, H-42b.

Chlamydomonas Ehrenberg 1833

1. *Chlamydomonas clathrata* (Korsh.) Pascher—N. C., pool on Yellow Mountain, elv. 5000 ft., Jackson Co. June 11, 1939, H-122. (There was another collection from the same site made three days later.)
2. *C. conversa* Korsh.—GA., pool off inlet to Chattooga River, Rabun Co. May 22, 1939, H-58.
3. *C. Ehrenbergii* Gorosh.—TENN., pool beside road near Strawberry Plains, Knox Co. June 30, 1938, B-24e.
4. *C. gloeogama* Korsh.—N. C., pasture pools near Phillips Lake, with *Carteria Fritschii* Takeda, Macon Co. May 15, 1939; S. C., pool near water trough near Walhalla, Oconee Co. May 21, 1939, H-56.
5. *C. yasuta* Korsh.—N. C., fish-rearing pools at Wolf Mt. Lumber Co. Club, Jackson Co. June 15, 1939, H-147.
6. *C. pseudopertyi* Pascher—TENN., swampy pool beside road near Strawberry Plains, Knox Co. June 30, 1938, B-24.

Chlorogonium Ehrenberg 1830

1. *Chlorogonium tetragamum* Bohlin—TENN., roadside ditch near Greenbrier Cove, Sevier Co. July 16, 1939, H-331.

Family *Phacotaceae*

Phacotus Perty 1852

1. *Phacotus angustus* Pascher—TENN., pool in brook near Laura Lake, Maury Co. Sept. 24, 1939, B-112.

2. *P. lenticularis* (Ehr.) Stein—TENN., plankton from Norris Lake, Campbell Co. June 21, 1938, Bold. (The species was previously reported from the state by Lackey, 1942.)

Family *Volvocaceae*

Pleodorina Shaw 1894

1. *Pleodorina californica* Shaw—TENN., permanent pond north of Tazewell, Claiborne Co. June 26, 1939, Bold.

Volvox Linnaeus 1758

1. *Volvox perglobator* Powers—TENN., permanent pond north of Tazewell, Claiborne Co. June 26, 1938, Bold.

Order TETRASPORALES

Family *Sphaerellaceae*

Sphaerella Sommerfelt 1824

1. *Sphaerella lacustris* (Girod) Wittr.—FLA., on submerged vegetation of Ashby Lake, Volusia Co. June 15, 1941, GP-1; TENN., bird bath at Beverly, Knox Co. July 7, 1938, Bold.

Stephanosphaera Cohn 1858

1. *Stephanosphaera pluviatilis* Cohn—N. C., rock pools on summit of Whiteside Mt., elv. 4900 ft., Jackson Co. June 4, 1939, H-95. (The only other report for southeastern United States was made from the same state by Whitford, 1943.)

Family *Palmellaceae*

Asterococcus Scherffel 1908

1. *Asterococcus limneticus* G. M. Smith—FLA., small pond near Florida highway 28 not far from Flagler Beach, Flagler Co. June 16, 1941; TENN., fish pool at Ijams' place, Knox Co. July 11, 1938, Bold.
2. *A. superbus* (Cienk.) Scherffel—N. C., Lake Sequoyah, Macon Co. May 23, 1939, Bold.

Gloeocystis Naegeli 1849

1. *Gloeocystis ampla* (Kuetz.) Lagerh.—TENN., permanent pond north of Tazewell, Claiborne Co. June 26, 1938, Bold, and on *Sphagnum* sp. at Ramsey Cascade, elv. 4150 ft., Sevier Co. July 18, 1939, Bold.
2. *G. confluens* (Kuetz.) P. Richt.—TENN., wet rocks beside trail near Newfound Gap, elv. 5500 ft., Sevier Co. S-610. (The writer has made other collections from similar habitats in the vicinity.)

Sphaerocystis Chodat 1897

1. *Sphaerocystis Schroeteri* Chod.—TENN., plankton from Norris Lake, Campbell Co. June 26, 1938, Bold.

Urococcus Kuetzing 1849

1. *Urococcus Hookerianus* Berk. & Hassall—TENN., limestone pools of small pool entering lake below high water mark of Norris Lake in Cove Creek inlet, Campbell Co. April 12, 1947, S-632.

Family *Tetrasporaceae*

Apiocystis Naegeli 1849

1. *Apiocystis Brauniana* Naeg.—S. C., on a cliff by Eastatoe River, Oconee Co. July 2, 1939, H-259a.

Schizochlamys A. Braun 1849

1. *Schizochlamys gelatinosa* A. Braun—N. C., in frog pond four miles west of Franklin, Macon Co. July 11, 1939, H-316.

Tetraspora Link 1809

1. *Tetraspora cylindrica* (Wahlb.) Agardh—TENN., attached to rocks in quiet river pool in Ramsey Prong, elv. 3250 ft., Sevier Co. Sept. 5, 1941, S-188.
2. *T. gelatinosa* (Vaucher) Desv.—N. C., roadside rocks, Jackson Co. June 6, 1939, H-110; TENN., Chilowee Park Lake at Knoxville, Knox Co. June 29, 1938, Bold.

Family *Coccomyxaceae*

Coccomyxa Schmidle 1901

1. *Coccomyxa dispar* Schm.—N. C., on partly submerged burned log in Phillips Lake, Macon Co. May 15, 1938, H-52.

Nannochloris Naumann 1919

1. *Nannochloris bacillaris* Naumann—TENN., bird bath at Beverly, Knox Co. June 19, 1938, Bold. (The species was also collected in a culture of fern prothallia at the University of Tennessee at Knoxville.)

Order ULOTRICHALES

Family *Ulotrichaceae*

Binuclearia Wittrock 1886

1. *Binuclearia tatrana* Wittr.—N. C., on aquatic angiosperms in Lake Sequoyah, Macon Co. May 22, 1939, H-72, and another collection from John Wesley Edwards Lake in Jackson Co. on June 20, 1939. (The only other report from southeastern United States was from the same state by Whitford, 1943.)

Stichococcus Naegeli 1849 emend. Gay 1891

1. *Stichococcus flaccidus* (Kuetz.) Gay—TENN., dried up puddle on bare soil of field at Booth Kennels, Knox Co. Mar. 18, 1947, S-519.
2. *S. fluitans* Gay—TENN., on mosses at Ramsey Cascade, elv. 4150 ft., Sevier Co. July 18, 1939, H-346.
3. *S. rivularis* (Kuetz.) Hazen—TENN., on wet rock ledge beside Ramsey Cascade, elv. 4200 ft., Dec. 28, 1946, H-417.

Ulothrix Kuetzing 1833

1. *Ulothrix aequalis* Kuetz.—TENN., on stones in brook near highway U. S. 70 at Kingston Springs, Davidson Co. Mar. 5, 1939, B-3947.
2. *U. tenuissima* Kuetz.—N. C., pools on Yellow Mt., elv. 5100 ft., Jackson Co. June 14, 1939, H-139; TENN., on stones in brook near highway U. S. 70 at Kingston Springs, Davidson Co. Mar. 5, 1939, B-3947.
3. *U. variabilis* Kuetz.—N. C., spring log at Moore's Cabin Spring on Gregory Bald, Graham Co. Jan. 26, 1942, S-202.

Order MICROSPORALES

Family *Microsporaceae*

Microspora Thuret 1850 emend. Lagerheim 1888

1. *Microspora amoena* (Kuetz.) Lagerh.—N. C., shallow water on south shore of Lake Sequoyah, Macon Co. May 22, 1939, H-60; TENN., on vegetable matter in roadside puddle southeast of Knoxville, elv. 1000 ft., Knox Co. Mar. 19, 1947, S-532.
2. *M. stagnorum* (Kuetz.) Lagerh.—S. C., Brown's Lake, pH 6.6, Mt. Rest, Oconee Co. June 12, 1939, H-123.
3. *M. Wittrockii* Lagerh.—GA., pool off outlet to Chattooga River, Rabun Co. May 22, 1939, H-59.

Order CYLINDROCAPSALES

Family *Cylindrocapsaceae*

Cylindrocapsa Reinsch 1867

1. *Cylindrocapsa geminella* Wolle—TENN., on *Cladophora* sp. in Hidden Lake, Davidson Co. Sept. 17, 1938, B-104a.

Order CHAETOPHORALES

Family *Chaetophoraceae*

Chaetophora Schrank 1789

1. *Chaetophora elegans* (Roth) Agardh—N. C., Ravenel Lake, Macon Co. May 13, 1939, H-36; TENN., globular jelly masses among weeds in water at Carter's Mill, Knox Co. April 2, 1947, S-560.

2. *C. incrassata* (Hudson) Hazen—TENN., Cunningham Lake, fed with small stream, near Clarksville, Montgomery Co. April 30, 1948, Alfred Clebsch-7.

Chlorotylium Kuetzing 1843

1. *Chlorotylium cataractarum* Kuetz.—TENN., in limestone pools below high water line at entrance of small stream to Cove Creek inlet of Norris Lake, Campbell Co. April 12, 1947, S-632.

Draparnaldia Bory 1808

1. *Draparnaldia acuta* (Agardh) Kuetz.—TENN., in clear, cold, moderately fast spring run-off in Fountain City Park, Knox Co. May 23, 1946.
2. *D. platyzonata* Hazen—TENN., on large rocks in Ramsey Prong, elv. 1600 ft., Sevier Co. Nov. 24, 1946, S-368.
3. *D. pulmosa* (Vaucher) Agardh—TENN., clear soil-bottomed pool of stream below Newfound Gap Highway, elv. 1700 ft., Sevier Co. April 20, 1947, S-607.

Microthamnion Naegeli 1849

1. *Microthamnion Kuetzingianum* Naeg.—TENN., clinging to rocks and humus in Porter's Prong, elv. 3500 ft., Sept. 6, 1941, Sevier Co. S-159.

Stigeoclonium Kuetzing 1843

1. *Stigeoclonium aestivale* (Hazen) Coll.—N. C., Kalalanta Swamp, Transylvania Co. June 5, 1939, H-102.
2. *S. attenuatum* (Hazen) Coll.—TENN., on propeller of ferryboat on river at Sweetwater, Monroe Co. July 7, 1938, Bold.
3. *S. lubricum* (Dillw.) Kuetz.—TENN., in roadside drain pH 4.5–5.0 beside Roaring Fork Road one half mile from Gatlinburg, Sevier Co. Nov. 24, 1946, S-348.
4. *S. nanum* (Dillw.) Kuetz.—FLA., plankton sample from Ashby Lake, Volusia Co. June 16, 1941, GP-2.
5. *S. tenue* (Agardh) Kuetz.—TENN., on submerged rocks in stream by Grassy Patch parking area, Sevier Co. Aug. 12, 1941, S-39.
6. *S. thermale* A. Braun—S. C., on board in still water, no date given, Rav-263.

Family *Protococcaceae*

Protococcus Agardh 1824

1. *Protococcus viridis* Agardh—TENN., on bark of tree near Avondale Springs, Grainger Co. May 5, 1947, S-591. (This species is so very common that few bother to report it, even for the sake of record.)

Family *Coleochaetaceae*

Chaetosphaeridium Klebahn 1892

1. *Chaetosphaeridium Pringsheimii* Klebahn—N. C., High Hampton Lake, pH 7.2, Jackson Co. June 2, 1939, H-87.

Coleochaete de Brébisson 1844

1. *Coleochaete irregularis* Prings.—TENN., permanent pond north of Tazewell, Claiborne Co. June 26, 1938, Bold.
2. *C. nitellarum* Jost—N. C., on *Nitella* sp. in High Hampton Lake, Jackson Co. July 12, 1939, H-326.
3. *C. orbicularis* Prings.—TENN., permanent pond north of Tazewell, Claiborne Co. June 26, 1938, Bold.
4. *C. pulvinata* A. Braun—S. C., plankton from Brown's Lake, pH 6.6, Oconee Co. June 12, 1939, H-123.
5. *C. scutata* (Bréb.) Prings.—N. C., Haywood Co. July 7, 1939, H-362a.

Family *Trentepohliaceae*

Trentepohlia Martius 1817

1. *Trentepohlia aurea* (L) Martius—N. C., rocks in lower Cullasaja Gorge, Macon Co. June 24, 1939, H-199.

Order SCHIZOGONIALES

Family *Schizogoniaceae*

Schizogonium Kuetzing 1843

1. *Schizogonium murale* Kuetz.—TENN., wet trailside rock 7.9 miles east of Newfound Gap, elv. 5500 ft., Sevier Co. Sept. 4, 1941, S-117.

Order CHLOROCOCCALES

Family *Endosphaeraceae*

Kentrosphaeria Borzi 1883

1. *Kentrosphaeria* sp.—N. C., rock pools at summit of Yellow Mountain, Jackson Co. June 14, 1939, B-141.

Family *Characiaceae*

Characium A. Braun 1849

1. *Characium Debaryanum* (Reinsch) DeToni—TENN., roadside pool, Jefferson Co. June 26, 1938, Bold.

Family *Protosiphonaceae*

Protosiphon Klebs 1896

1. *Protosiphon botryoides* (Kuetz.) Klebs—TENN., on a stick in mixed stream and backwater of Ft. Loudon Lake (Tennessee River) below Knoxville, Knox Co. April 5, 1947, S-584.

Family *Hydrodictyaceae*

Hydrodictyon Roth 1800

1. *Hydrodictyon reticulatum* (L) Lagerh.—TENN., spring-fed lake at Orphans' Home, Spring Hill, Maury Co. Sept. 24, 1938, B-117b.

Family *Coelastraceae*

Coelastrum Naegeli 1849

1. *Coelastrum proboscideum* Bohlin—N. C., Fairfield Lake, Jackson Co. August 4, 139, H-415.

Family *Oocystaceae*

Ankistrodesmus Corda 1838 emend. Ralfs 1848

1. *Ankistrodesmus falcatus* (Corda) Ralfs—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.
2. *A. spiralis* (Turner) Lemm.—TENN., fish-rearing pools below Norris Dam, Anderson Co. June 26, 1938, Bold.

Chlorella Beyerinck 1890

1. *Chlorella conductrix* Brandt—FLA., in pond near Osteen, Volusia Co. June 15, 1941, GP-6.

Dimorphococcus A. Braun 1855

1. *Dimorphococcus lunatus* A. Braun—TENN., in lily pool on campus of Vanderbilt University, Nashville, Davidson Co. Nov. 12, 1938, B-154a.

Eremosphaera De Bary 1858

1. *Eremosphaera viridis* De Bary—S. C., plankton from Brown's Lake, Mt. Rest, Oconee Co. May 21, 1939, H-69, and the same site on June 12, 1939; FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.

Kirchneriella Schmidle 1893

1. *Kirchneriella lunaris* (Kirch.) Moebius—GA., cliff pool near Clayton, Rabun Co. July 5, 1939, H-288.

Nephrocytium Naegeli 1849

1. *Nephrocytium Agardhianum* Naeg.—TENN., permanent pond north of Tazewell, Claiborne Co. June 26, 1938, Bold.

Oocystis Naegeli 1845

1. *Oocystis Borgei* Snow—FLA., on vegetation in pond near Osteen, Volusia Co., Jan. 15, 1941, GP-1.
2. *O. elliptica* W. West—N. C., gelatinous coating on wet rock at Bridal Veil Falls, Macon Co. May 14, 1939, H-41a.
3. *O. lacustris* Chod.—FLA., in small pond near Florida state highway 28 near Flagler Beach, Flagler Co. June 16, 1941, GP-10.
4. *O. rupestris* Kirch.—TENN., in rock pools at Ramsey Cascade, elv. 4150 ft., Sevier Co. July 18, 1939.

Selenastrum Reinsch 1867

1. *Selenastrum minutum* (Naeg.) Coll.—TENN., in fish pool on Sanford Estate, Knoxville, Knox Co. July 7, 1938, Bold.

Family *Scenedesmaceae*

Scenedesmus Meyen 1829

1. *S. longus* var. *ellipticus* (West & West) G. M. Smith—FLA., on submerged aquatics and on ground at edge of small lake near Osteen, Volusia Co. June 15, 1941, GP-9.
2. *S. quadricauda* var. *dispar* Bréb.—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-6.
3. *S. quadricauda* var. *quadrispina* (Chodat) G. M. Smith—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.

Family *Botryococcaceae*

Botryococcus Kuetzing 1849

1. *Botryococcus Braunii* Kuetz.—TENN., fish-rearing pools below Norris Dam, Anderson Co. June 26, 1938, Bold.

Order OEDOGONIALES

Family *Oedogoniaceae*

Bulbochaete Agardh 1817

1. *Bulbochaete minor* A. Braun—N. C., on *Sphagnum* sp. beside Toxaway River, Transylvania Co. June 6, 1939, H-104.

Oedogonium Link 1820

1. *Oedogonium crenulatocostatum* Wittr.—TENN., Buffalo Springs, Grainger Co. June 26, 1938, B-14a & b.
2. *O. decipiens* var. *dissimile* (Hirn) Tiff.—N. C. on *Sphagnum* sp. at edge of Toxaway River, Transylvania Co. June 6, 1939, H-104.
3. *O. Hirnii* Gutw.—TENN., in ditch near Cosby, Cocke Co. July 17, 1939, H-366.
4. *O. irregulare* var. *condensatum* (Hallas) Hirn—S. C., on wooden dock at Brown's Lake, Mt. Rest. Oconee Co. June 12, 1939, B-124.
5. *O. multisporum* Wood—N. C., on *Sphagnum* sp. at edge of Toxaway River, Transylvania Co. June 6, 1939, H-104.
6. *O. plagiostomum* Wittr.—TENN., permanent pond north of Tazewell, Claiborne Co. June 26, 1939, Bold.

Order SIPHONOCLADALES

Family *Cladophoraceae*

Basicladia Hoffman & Tilden 1930

1. *Basicladia chelonum* (Coll.) Hoff. & Tilden—TENN., from turtle in pond near Kimberlin Heights, Knox Co. June 22, 1938.

Cladophora Kuetzing 1843

1. *Cladophora crispata* (Roth) Kuetz.—TENN., limestone pools at entrance of small stream to Norris Lake in Cove Creek inlet, Campbell Co. April 12, 1947, S-628.

Pithophora Wittrock 1877

1. *Pithophora varia* Wille—TENN., aquarium at University of Tennessee, May 16, 1947, S-692.

Rhizoclonium Kuetzing 1843

1. *Rhizoclonium crispum* Kuetz.—TENN., aquarium at University of Tennessee Botany Department, Knoxville, Knox Co. July 7, 1938, Bold.

Order SIPHONALES

Family *Vaucheriaceae*

Dichotomosiphon Ernst 1902

1. *Dichotomosiphon tuberosus* (A. Braun) Ernst—TENN., Montvale Springs Lake, Blount Co. June 30, 1931, Bold.

Vaucheria DeCandolle 1803

1. *Vaucheria arrhyncha* Heid.—S. C., on moist rocks in Eastatoe River, Oconee Co. July 2, 1939, H-267.
2. *V. geminata* f. *racemosa* (Vaucher) Walz—TENN., in shallows of brook, Deacon Creek, Brentwood, Williamson Co. Dec. 30, 1938, B-3914.
3. *V. repens* Hassall—TENN., dam at Centennial Park Lake, Nashville, Davidson Co. Nov. 3, 1938, B-182.
4. *V. sessilis* (Vaucher) De Cand.—TENN., in stream running over bank beside road near Sugarlands C. C. C. Camp site, elv. 1600 ft., Sevier Co. April 20, 1947.
5. *V. terrestris* Lyngbye—N. C., on wet rocks below Lickstone Bald, Haywood Co. July 17, 1939, H-363. (The only other report from southeastern United States was from the same state by Whitford, 1943.)

Order ZYGNEMATALES

Family *Zygnemataceae*

Spirogyra Link 1820

1. *Spirogyra communis* (Hassall) Kuetz.—N. C., on dripping rock, Jackson Co. June 1, 1939, H-85.
2. *S. denticulata* Trans.—TENN., floating in calcareous rock pool near highway U. S. 70, Rutherford Co. May 17, 1939, B-2937.
3. *S. laxa* Kuetz.—N. C., on vegetation near dock on Sapphire Lake, Jackson Co. June 9, 1939, H-114.
4. *S. longata* (Vaucher) Kuetz.—N. C., on vegetation near dock on Sapphire Lake, Jackson Co. June 9, 1939, H-114.

5. *S. miamiana* Taft—FLA., attached to submerged tin can near shore of Ashby Lake, Volusia Co. June 16, 1941, GP-3.
6. *S. parvula* (Trans.) Czurda—N. C., Small Lake, Macon Co. June 20, 1939, Bold.
7. *S. Spreeiana* Rab.—TENN., pool near Glen Echo Lake, Davidson Co. Feb. 19, 1939, B-3935.

Zygogonium Kuetzing 1843

1. *Zygogonium ericetorum* Kuetz.—TENN., in frozen puddle on Sugarlands Mountain trail near Mt. Collins, Sevier Co. Dec. 7, 1946, S-452.

Family *Mesotaeniaceae*

Cylindrocystis Meneghini 1838

1. *Cylindrocystis americana* West & West—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.
2. *C. Brebissonii* Menegh.—N. C., in brownish floating gelatinous masses in shallow water of Ravenel Lake, Macon Co. May 12, 1939, H-35.

Mesotaenium Naegeli 1849

1. *Mesotaenium chlamydosporum* var. *minor* Reinsch—N. C., at dam on Phillips Lake, Macon Co. May 15, 1939, H-46.
2. *M. Greyi* Turner—N. C., on mosses in dripping cliffs at Buttermilk Falls, Macon Co. June 18, 1939, H-170.
3. *M. macrococcum* (Kuetz.) Roy—TENN., on wet *Thuidium* sp. at Carter's Farm, elv. 1100 ft., Knox Co. Oct., 1947, Silva (Iltis)-700.
4. *M. mirificum* Archer—N. C., rock pools on summit of Whiteside Mt., Jackson Co. June 4, 1939, H-96.

Roya West & West 1898 emend. Hodgetts 1920

1. *Roya obtusa* var. *montana* Gutw.—TENN., in rock pools at Ramsey Cascade, elv. 4150 ft., Sevier Co. July 18, 1939, H-334.

Spirotaenia de Brébisson 1848

1. *Spirotaenia eboracensis* West apud. Luetkemueller—S. C., east-facing cliff dripping with water, near Walhalla, Oconee Co. May 21, 1939, H-61.

Family *Desmidiaceae*

Arthrodesmus Ehrenberg 1838

1. *Arthrodesmus incus* var. *validus* West & West—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1. (The only other report from southeastern United States was made from the same state by West & West, 1898.)

Closterium Nitzsch 1817

1. *Closterium acerosum* (Schrank) Ehr.—TENN., loose coating on marble pebbles in spring at Fountain City Park, Knox Co. Mar. 23, 1946, S-549.
2. *C. didymotocum* Corda—N. C., in brown debris at Ravenel Lake, Macon Co. May 13, 1939, H-36.
3. *C. incurvum* Bréb.—N. C., High Hampton Lake, Jackson Co. June 2, 1939, H-87.
4. *C. intermedium* Ralfs—N. C., on shallow bottom of Philips Lake, Macon Co. May 15, 1939, H-49.
5. *C. juncidum* Ralfs—N. C., on shallow bottom of Philips Lake, Macon Co. May 15, 1939, H-49.
6. *C. Kuetzingii* var. *vittatum* Nordst—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1939, GP-1.
7. *C. moniliferum* (Bory) Ehr.—TENN., in branch two miles below Norris Dam, Anderson Co. June 26, 1939, B-12.
8. *C. parvulum* var. *angustum* West & West—FLA., in plankton sample from Ashby Lake, Volusia Co. June 15, 1941, GP-2. (The other report from the state was by West & West, 1898.)
9. *C. pusillum* Hantzsch—N. C., pools at the summit of Yellow Mountain, elv. 5200 ft., Jackson Co. June 14, 1939, H-139.
10. *C. Ralfsii* var. *Imanne* Cush.—N. C., arm of Sapphire Lake causing red coloring of water, Jackson Co. June 9, 1939, H-177; S.C., at shore at upper end of Brown's Lake, Mt. Rest, Oconee Co. June 12, 1939, H-125.
11. *C. tozon* W. West—S. C., at shore of Brown's Lake, Mt. Rest, Oconee Co. June 12, 1939, H-125.
12. *C. tumidum* Johnson—S. C., branch in field by Walhalla Road, Oconee Co. May 21, 1939, H-60.
13. *C. ulna* Focke—N. C., Sapphire Lake, Jackson Co. June 9, 1939, H-117; S. C., pool near Bull Pen Road Bridge over Chattooga River, Oconee Co. July 30, 1939, H-386.
14. *C. Venus* Kuetz.—TENN., Hidden Lake, Davidson Co. Sept. 17, 1938, B-103.

Cosmarium Corda 1834

1. *Cosmarium angulosum* Bréb.—FLA., on submerged aquatics and on ground at edge of small lake near Osteen, Volusia Co. June 15, 1941, GP-9.
2. *C. Baileyi* Wolle—TENN., Chilowee Park Lake at Knoxville, Knox Co. July 15, 1938, Bold.
3. *C. isthmium* West—N. C., High Hampton Lake, pH 7.2, Jackson Co. June 2, 1939, H-87.
4. *C. Lundellii* var. *ellipticum* West—N. C., Ravenel Lake, Macon Co. May 13, 1939, H-37.
5. *C. microsphinctum* Nordst.—GA., east-facing cliff by Walhalla Road, Rabun Co. May 21, 1939, H-61.

6. *C. ocellatum* Eich. & Gutw.—GA., west-facing cliff by Walhalla Road, Rabun Co. May 21, 1939, H-62.
   Flagler Beach, Flagler Co. June 16, 1941, GP-10.
7. *C. orthostichum* var. *pumilum* Lund.—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-7.
8. *C. Pokornyanum* (Grunow) West & West—N. C., on west-facing cliff, Jackson Co. May 7, 1939, H-33.
9. *C. Portianum* var. *nephroideum* Wittr.—FLA., on submerged aquatics and on the ground at edge of small lake near Osteen, Volusia Co. June 15, 1941, GP-9.
10. *C. punctulatum* Bréb.—TENN., Miss Littleton's lily pool, Kingston, Roane Co. July 8, 1938, Bold.
11. *C. reniforme* (Ralfs) Arch.—TENN., pond on Maryville Pike near city limits of Knoxville, Knox Co. June 30, 1931, Bold.
12. *C. subcucumis* Schm.—N. C., Ravenel Lake, Macon Co. May 24, 1939, H-82; FLA., small pond near Florida state highway 28, Flagler Co. June 16, 1941, GP-10.
13. *C. subtumidum* Nordst.—MISS., in big water fountain near Post Office, Vicksburg, Warren Co. Sept. 2, 1945, Delzie Demaree-25478.
14. *C. undulatum* var. *minutum* Wittr.—N. C., on wet west-facing cliff, Jackson Co. May 7, 1939, H-33.
15. *C. undulatum* var. *Wollei* West—GA., east-facing cliff by Walhalla Road, Rabun Co. May 21, 1939, H-61.

Desmidium Agardh 1825

1. *Desmidium Baileyii* var. *minor* Allorge & Allorge—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1; TENN., Miss Littleton's lily pool, Kingston, Roane Co. July 8, 1938, Bold.
2. *D. Grevillii* (Kuetz.) De Bary—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-4.

Euastrum Ehrenberg 1832 emend. Ralfs 1844

1. *Euastrum binale* var. *Groenbladii* Krieger—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.
2. *E. crassum* var. *scrobiculatum* Lund.—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.
3. *E. didelta* (Turpin) Ralfs—N. C., ditch in field at Hull Home, Macon Co. June 1, 1939, H-90.
4. *E. insigne* var. *lobatum* Prescott & Scott—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1939, GP-4.
5. *E. oblongum* (Grev.) Ralfs—TENN., permanent pond north of Tazewell, Claiborne Co. June 26, 1938, Bold.
6. *E. sinuosum* Lenor.—N. C., on seeping rocks by Toxaway River, Transylvania Co. June 6, 1939, H-104.

7. *E. Turnerii* West—N. C., High Hampton Lake, Jackson Co. June 2, 1939, H-87.
8. *E. validum* West & West—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-5.
9. *E. verrucosum* var. *sublatum* Bréb.—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-4.

Gymnozyga Ehrenberg 1841

1. *Gymnozyga Brebissonii* (Kuetz.) Wille—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.

Hyalotheca Ehrenberg 1841

1. *Hyalotheca dissiliens* (Smith) Bréb.—TENN., McMinnville, Warren Co. Feb. 7, 1938, Bold (Miss Mason).
2. *H. mucosa* (Dillw.) Ehr.—TENN., Lakeside Pond, Sevierville Pike, Knox Co. July 11, 1938.
3. *H. mucosa* var. *minor* Roy—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.
4. *H. undulata* Nordst.—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-7.

Micrasterias Agardh 1827

1. *Micrasterias americana* (Ehr.) Ralfs—TENN., McMinnville, Warren Co. Jan. 2, 1938, Bold (Miss Mason).
2. *M. apiculata* (Ehr.) Menegh.—VA., edge and bottom of old reservoir at University of Virginia at Charlottesville, Albemarle Co. Oct. 7, 1939, Strickland (G. H. Binnoveld); TENN., McMinnville, Warren Co. Jan. 2, 1938, Bold (Miss Mason).
3. *M. denticulata* var. *angustosinuata* Gay—N. C., ditch in field near Hull Home, Macon Co. June 1, 1939, H-90.
4. *M. depauperata* var. *Wollei* Cush.—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1939, GP-7.
5. *M. muricata* (Bailey) Ralfs—N. C., Sapphire Lake, Jackson Co. June 9, 1939, Bold.
6. *M. muricata* var. *simplex* Groen.—FLA., on submerged aquatics and on ground at edge of small lake near Osteen, Volusia Co. June 15, 1939, GP-9.
7. *M. oscitans* Ralfs—N. C., in swamp by Watauga River, Watauga Co., summer 1939, H-700a.
8. *M. oscitans* var. *mucronata* (Dixon) Wille—FLA., in plankton sample from Ashby Lake, Volusia Co. June 16, 1941, GP-2.
9. *M. radiata* Hassall—TENN., Miss Littleton's lily pool at Kingston, Roane Co. July 11, 1938, Bold.
10. *M. radiata* var. *gracillima* G. M. Smith—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.
11. *M. radiosa* Ralfs—N. C., Sapphire Lake, Jackson Co. June 9, 1939, H-117.

12. *M. radiosa* var. *ornata* Nordst.—S. C., in plankton from Brown's Lake, Mt. Rest, Oconee Co. May 21, 1939, and June 12, 1939, Bold.
13. *M. truncata* (Corda) Bréb.—TENN., Miss Littleton's lily pool at Kingston, Roane Co. July 11, 1938, Bold.
14. *M. truncata* var. *granulata* Racib.—N. C., Ravenel Lake, Macon Co. May 10, 1939, and May 13, 1939, H-37.
15. *M. truncata* var. *tridentata* Krieger—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.

Onychonema Wallich 1860

1. *Onychonema laeve* var. *latum* West & West—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.

Penium de Brébisson 1844

1. *Penium cucurbitinum* Bissett—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-7.
2. *P. cylindrus* (Ehr.) Bréb.—N. C., gelatinous coating on wet rocks at Bridal Veil Falls, Macon Co. May 14, 1939, H-41a.
3. *P. libellula* (Focke) Nordst.—N. C., shallow water in upper Sapphire Lake, Jackson Co., June 9, 1939, H-117.
4. *P. Margaritaceum* (Ehr.) Bréb.—TENN., roadside pool, Jefferson Co. June 26, 1938, Bold.
5. *P. spirostriolatum* Barker—N. C., rock pools at the summit of Yellow Mountain, Jackson Co. June 14, 1939, H-142.

Phymatodocis Nordstedt 1877

1. *Phymatodocis Nordstedtiana* Wolle—VA., thick gelatinous masses attached to *Utricularia* sp. in slow-moving water of small pond run-off 10 miles south of Fredericksburg, Caroline Co. Sept. 9, 1947, Iltis-3692.

Pleurotaenium Naegeli 1849

1. *Pleurotaenium maximum* (Reinsch) Lund.—N. C., Ravenel Lake, Macon Co. May 13, 1939, H-37.
2. *P. minutum* (Ralfs) Delp.—N. C., shallow bottom in Phillips Lake, Macon Co. May 15, 1939, H-43.
3. *P. minutum* var. *elongatum* West & West—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.
4. *P. minutum* var. *major* Lund—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.
5. *P. nodosum* (Bailey) Lund.—N. C., in swamp along Cave Creek, Haywood Co. July 17, 1939, H-362.
6. *P. trabecula* (Ehr.) Naeg.—TENN., roadside pool, Jefferson Co. June 26, 1938, Bold.
7. *P. trochiscum* var. *tuberculatum* G. M. Smith—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-5.

Spondylosium de Brébisson 1844

1. *Spondylosium pygmaeum* (Rab.) West—N. C., swamp along Watauga River, Watauga Co. summer 1939, H-700a.

Staurastrum Meyen 1829

1. *Staurastrum anatinum* var. *longibrachiatum* West & West—FLA., on submerged aquatics and on ground at edge of small lake near Osteen, Volusia Co. June 15, 1941, GP-9.
2. *S. Archerii* West—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-7.
3. *S. brasiliense* var. *Lundellii* West & West—S. C., Brown's Lake, pH 6.6 at Mt. Rest, Oconee Co. June 12, 1939, H-125.
4. *S. capitulum* Bréb.—N. C., Bridal Veil Falls, Macon Co. May 14, 1939, H-41.
5. *S. connatum* (Lund.) Roy & Bissett—FLA., small pond near Florida state highway 28 near Flagler Beach, Flagler Co. June 16, 1939, GP-10.
6. *S. elongatum* var. *quadratum* Irénée-Marie—FLA. on submerged aquatics and on ground at edge of small lake near Osteen, Volusia Co. June 15, 1941, GP-9.
7. *S. furcatum* var. *pisciforme* Turner—FLA., small pond near Florida state highway 28 near Flagler Beach, Flagler Co. June 16, 1941, GP-10.
8. *S. gladiosum* Turner—N. C., Fox Swamp, Macon Co. June 2, 1939, H-102.
9. *S. gracile* var. *nanum* Wille—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.
10. *S. gracile* var. *tenuissimum* Boldt—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-5.
11. *S. grande* Bulnh.—S. C., Brown's Lake, pH 6.6, Mt. Rest, Oconee Co. May 21, 1939, Bold.
12. *S. grande* var. *parvum* West—FLA., on submerged aquatics and on ground at edge of small lake near Osteen, Volusia Co. June 15, 1941, GP-1.
13. *S. gyrans* Johnson—FLA., small pond near Florida state highway 28 near Flagler Beach, Flagler Co. June 16, 1941, GP-10.
14. *S. hexacerum* (Ehr.) Wittr.—N. C., Bridal Veil Falls, Macon Co. May 14, 1939, H-41; FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-7.
15. *S. lacustre* G. M. Smith—FLA., on submerged aquatics and on ground at edge of small lake near Osteen, Volusia Co. June 15, 1941, GP-9.
16. *S. Meriani* Reinsch.—N. C., on rocks near highway U. S. 64, Macon Co. June 1, 1939, H-83.
17. *S. muticum* Bréb.—N. C., plankton from High Hampton Lake, Jackson Co. June 2, 1939, H-86a.
18. *S. ophiura* var. *minus* Prescott & Scott—FLA., on vegetation in pond near Osteen, Volusia Co. June 15, 1941, GP-5.
19. *S. orbiculare* var. *hibernicum* W. West—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.

20. *S. pachyrhynchum* Nordst.—FLA., on submerged aquatics and on ground at edge of small lake near Osteen, Volusia Co. June 15, 1941, GP-9.
21. *S. paradoxum* Meyen—TENN., Chilowee Park Lake at Knoxville, Knox Co. July 15, 1938, Bold.
22. *S. pyramidatum* West—FLA., on submerged vegetation in Ashby Lake, Volusia Co. June 15, 1941, GP-1.
23. *S. turgescens* de Not.—N. C., on wet west-facing cliff, Jackson Co. May 7, 1938, H-33.

Tetmemorus Ralfs 1844

1. *Tetmemorus Brebissonii* var. *minor* De Bary—FLA., attached to submerged vegetation in pond near Osteen, Volusia Co. June 16, 1941, GP-4.
2. *T. granulatus* (Bréb.) Ralfs—N. C., pasture pools near Phillips Lake, Macon Co. May 15, 1939, H-53.

Xanthidium Ehrenberg 1837

1. *Xanthidium antilopaeum* var. *polymazum* Nordst.—N. C., in shallow water on east side of Phillips Lake, Macon Co. May 15, 1939, H-43.
2. *X. armatum* (Bréb.) Rab.—N. C., on seeping rocks in Toxaway River, Transylvania Co. June 6, 1939, H-104.
3. *X. armatum* var. *mediolaeve* G. M. Smith—FLA., in small pond near Florida state highway 28 near Flagler Beach, Flagler Co. June 16, 1941, GP-10.
4. *X. pseudobengalicum* Groenb.—FLA., in small pond near Florida state highway 28 near Flagler Beach, Flagler Co. June 16, 1941, GP-10.
5. *X. Robinsonianum* var. *parvulum* Skuja—FLA., in small pond near Florida state highway 28 near Flagler Beach, Flagler Co. June 16, 1941, GP-10.

Order CHARALES

Family *Characeae*

Chara Linnaeus 1754

1. *Chara gymnopus* A. Braun—VA., growing in sand at edge of Shenandoah River, Warren Co. Sept. 9, 1945, H. G. Diegman-701.

Phylum EUGLENOPHYTA

Class **Euglenophyceae**

Order EUGLENALES

Family *Euglenaceae*

Euglena Ehrenberg 1838

1. *Euglena acutissima* Lemm.—TENN., pond on old Sevierville Pike near Kimberlin Heights, Knox Co. June 22, 1938, Bold.
2. *E. deses* Ehr.—S. C., Brown's Lake at Mt. Rest, Oconee Co. May 21, 1939, H-69a.
3. *E. gracilis* Klebs—TENN., Sanford Estate at Knoxville, Knox Co. July, 1938, Bold.

4. *E. polymorpha* Dang.—N. C., Phillips Lake, Macon Co. May 15, 1939, H-49.
5. *E. splendens* Dang.—TENN., Andrew Jackson (Dead Horse) Lake, Knox Co. July 7, 1938, Bold.
6. *E. tripteris* (Duj.) Klebs—TENN., Chilowee Park Lake at Knoxville, Knox Co. June 26, 1938, Bold.

Phacus Dujardin 1841

1. *Phacus caudatus* Hueb.—TENN., Montvale Springs Lake, Blount Co. June 30, 1931, Bold.
2. *P. orbicularis* Hueb.—TENN., Chilowee Park Lake at Knoxville, Knox Co. June 29, 1938.

Phylum PYRROPHYTA

Class **Dinophyceae**

Order PERIDINIALES

Family *Gonyaulaceae*

Gonyaulax Diesing 1866 emend. Kofoid 1911

1. *Gonyaulax palustris* Lemm.—TENN., Fountain City Park Lake, Knox Co. July 12, 1938, Bold.

Phylum RHODOPHYTA

Class **Rhodophyceae**

SUB-CLASS PROTOFLORIDEAE

Order BANGIALES

Family *Porphyridiaceae*

Porphyridium Naegeli 1849

1. *Porphyridium cruentum* Naeg.—TENN., on wet sand in greenhouse at University of Tennessee at Knoxville, Knox Co. May 7, 1947, S-694.

SUB-CLASS FLORIDEAE

Order NEMALIONALES

Family *Batrachospermaceae*

Batrachospermum Roth 1797

1. *Batrachospermum Boryanum* Sirodot—TENN., Carter's Mill Spring, Knox Co. April 2, 1947, S-572.
2. *B. densum* Sirodot—TENN., Fountain City Park Lake, Knox Co. July 12, 1938, Bold.
3. *B. moniliforme* Roth—TENN., in small sluiceway from stream running through gravel and peat on Porter's Prong, elv. about 3300 ft., Sevier Co. Sept. 4, 1941, S-155.

4. *B. sporulans* Sirodot—N. C., on rocks in culvert three miles west of Highlands, Macon Co. May 15, 1939, H-45.

Lemanea Bory 1808 emend. Agardh 1838

1. *Lemanea* (*Sacheria*) *fluviatilis* Agardh.—TENN., on sandstone brink of Falls Creek Falls, Van Buren Co. May 4, 1947, S-668.

Tuomeya Harvey 1858

1. *Tuomeya fluviatilis* Harvey—TENN., on sandstone brink of Falls Creek Falls, Van Buren Co. May 4, 1947, S-668.

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SOME PROPERTIES OF THE GENERALIZED LOGOCYCLIC CURVE AND CERTAIN ASSOCIATED CURVES

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1. *Introduction.* Consider the plane curve λ_t whose rectangular coordinates are given as follows:

$$x = \rho \cos(t\theta), \qquad y = \rho \sin(t\theta); \tag{1}$$

where $\rho = a(\sec\theta \pm \tan\theta)$, a is a positive constant, θ is a variable such that $-\frac{\pi}{2} \leqq \theta \leqq \frac{\pi}{2}$, t is a real number. It is sufficient to take $t \geqq 0$, since θ may assume negative values. For a given value of t, equations (1) represent a curve symmetric with respect to the x-axis, passing through the origin, and having a double point at $(a, 0)$. For $t = 0$, the curve λ_0 is the positive half of the x-axis, including the origin.

From the definition of ρ, it is evident that for a given t and θ, equations (1) give two points of the curve λ_t. If we let ρ and $\bar{\rho}$ represent $a(\sec\theta + \tan\theta)$ and $a(\sec\theta - \tan\theta)$, respectively, then (1) may be written as:

$$\begin{aligned} x &= \rho \cos(t\theta), \qquad y = \rho \sin(t\theta); \\ \bar{x} &= \bar{\rho} \cos(t\theta), \qquad \bar{y} = \bar{\rho} \sin(t\theta). \end{aligned} \tag{1'}$$

The two points $P(x, y)$ and $\bar{P}(\bar{x}, \bar{y})$ so defined are a pair of corresponding inverse points with respect to the circle $x^2 + y^2 = a^2$.

Associated with each λ_t curve, $t \neq 0$, are two other curves, Γ_t and Ω_t, analytically defined in section 2, below, but which may be intuitively described as follows: Γ_t denotes the locus of the point of intersection of the tangents to λ_t at a pair of corresponding inverse points P and $\bar{P}$ as θ varies over its range; Ω_t represents the locus of the point of intersection of the corresponding normals.

James Booth[1] has found some interesting relations among the three curves λ_t, Γ_t and Ω_t when $t = 1$. As we shall show later, in section 2, these are the *logocyclic curve*,[2] the cissoid and the parabola, respectively (see figure 1). In fact, the λ_1 curve is commonly designated the strophoid; but Booth more appropriately called it the logocyclic curve on account of its relation to the theory of logarithms. Since we are dealing with a generalization of these three curves, it seems fitting to call λ_t the *generalized logocyclic curve*.

2. *Tangents and normals.* We now derive analytical expressions defining Γ_t and Ω_t. Using equations (1'), and letting t be fixed, we find that

[1] James Booth: Some New Geometrical Methods, Vol. I, Longmans, Green, 1873.
[2] *Ibid.*

$$dy = \rho[\sec\theta \sin(t\theta) + t\cos(t\theta)]\,d\theta,$$
$$dx = \rho[\sec\theta \cos(t\theta) - t\sin(t\theta)]\,d\theta,$$

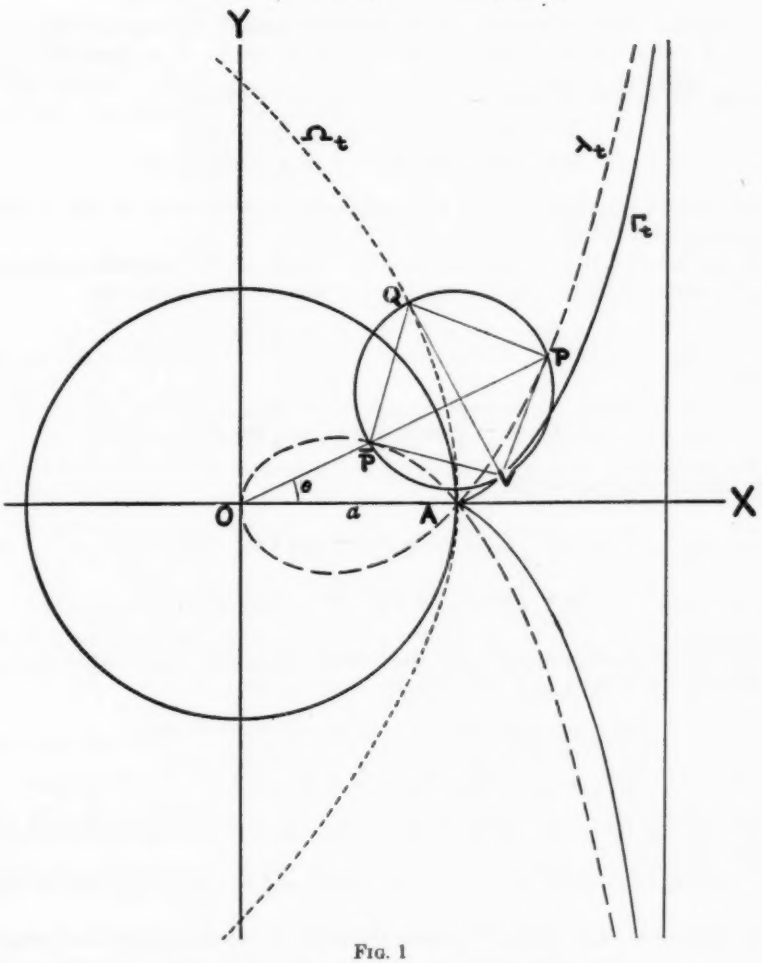

FIG. 1

since $d\rho = a(\sec\theta\tan\theta + \sec^2\theta)d\theta = \rho\sec\theta\,d\theta$. Therefore, the slope of the tangent to λ_t at $P(x, y)$ is

$$\frac{dy}{dx} = \frac{t + \sec\theta\tan(t\theta)}{\sec\theta - t\tan(t\theta)}, \qquad -\frac{\pi}{2} < \theta < \frac{\pi}{2}.$$

Similarly, it may be seen that

$$\frac{d\bar{y}}{d\bar{x}} = \frac{\sec\theta\tan(t\theta) - t}{\sec\theta + t\tan(t\theta)}.$$

If (X, Y) denotes a variable point on the tangents, then the equation of the tangent at P is $AX + BY = C$, and at $\bar{P}$ it is $\bar{A}X + \bar{B}Y = \bar{C}$, where

$$A = t + \sec\theta \tan(t\theta), \quad B = t\tan(t\theta) - \sec\theta, \quad C = \rho t \sec(t\theta);$$
$$\bar{A} = t - \sec\theta \tan(t\theta), \quad \bar{B} = t\tan(t\theta) + \sec\theta, \quad \bar{C} = \bar{\rho} t \sec(t\theta).$$

Solving this system of equations for X and Y, we obtain

$$X = a[\sec\theta \cos(t\theta) + t \sin\theta \sin(t\theta)], \tag{2}$$
$$Y = a[\sec\theta \sin(t\theta) - t \sin\theta \cos(t\theta)].$$

For a given t, equations (2) are the parametric representation of the Γ_t curve associated with the given λ_t.

In like manner, if (ξ, η) denotes a variable point on the normals to a λ_t at a pair of corresponding inverse points, the equations of the normals are

$$B\xi - A\eta = C' \text{ and } \bar{B}\xi - \bar{A}\eta = \bar{C}',$$

where

$$C' = -\frac{C}{t}\sec\theta \text{ and } \bar{C}' = \frac{\bar{C}}{t}\sec\theta.$$

Solving this system, we get

$$\xi = \frac{a}{t}\sec\theta\,[t\cos(t\theta) - \tan\theta \sin(t\theta)], \tag{3}$$
$$\eta = \frac{a}{t}\sec\theta\,[\tan\theta\cos(t\theta) + t\sin(t\theta)],$$

as the parametric representation of the corresponding Ω_t curve, if $t \neq 0$.

Putting $t = 1$ in (1), (2) and (3), one easily obtains

$$\lambda_t\colon\ x = a(1 \pm \sin\theta), \quad y = a(1 \pm \sin\theta)\tan\theta;$$
$$\Gamma_1\colon\ X = a(1 + \sin^2\theta), \quad Y = a\sin^2\theta\tan\theta;$$
$$\Omega_1\colon\ \xi = a(1 - \tan^2\theta), \quad \eta = 2a\tan\theta.$$

More familiar forms are obtained by eliminating θ, and using x and y in each case. They are
$(x^2 + y^2)(2a - x) = a^2x$; $(x - a)^3 = (2a - x)y^2$; and $y^2 = 4a(a - x)$, respectively.

3. *Theorems.* Let $V(X, Y)$ denote the point of intersection of the tangents to λ_t at a pair of corresponding inverse points P and $\bar{P}$; let $Q(\xi, \eta)$ represent the intersection of the normals at these points. We now prove the following

THEOREM I. *Any point V is equidistant from its pair of corresponding inverse points P and $\bar{P}$; likewise, Q is equidistant from P and $\bar{P}$.*

PROOF: The differences of the coordinates of V, P and $V, \bar{P}$ are

$$X - x = a[t\sin\theta\sin(t\theta) - \tan\theta\cos(t\theta)],$$
$$Y - y = -a[t\sin\theta\cos(t\theta) + \tan\theta\sin(t\theta)];$$
$$X - \bar{x} = a[t\sin\theta\sin(t\theta) + \tan\theta\cos(t\theta)],$$
$$Y - \bar{y} = -a[t\sin\theta\cos(t\theta) - \tan\theta\sin(t\theta)].$$

Squaring and adding these in pairs, we have the relation

$$(X - x)^2 + (Y - y)^2 = (X - \bar{x})^2 + (Y - \bar{y})^2,$$

which proves the first part of the theorem. The second part is proved in a similar manner.

THEOREM II. *The tangent to Ω_t at Q is perpendicular to the chord $P\bar{P}$.*

PROOF: The slope of the tangent to Ω_t at Q is obtained as follows:

$$d\eta = \frac{a}{t}(t^2 + 1 + 2\tan^2\theta)\sec\theta\cos(t\theta)\,d\theta,$$

$$d\xi = -\frac{a}{t}(t^2 + 1 + 2\tan^2\theta)\sec\theta\sin(t\theta)\,d\theta.$$

From these we get

$$\frac{d\eta}{d\xi} = -\cot(t\theta).$$

But the slope of the chord $P\bar{P}$ is $\tan(t\theta)$. Therefore, the two lines are perpendicular.

COROLLARY I. *The tangent to Ω_t at Q passes through the corresponding V of Γ_t.*

The proof follows from theorems I and II. We also have the following

COROLLARY II. *Line segment VQ is a diameter of a circle passing through P and $\bar{P}$.*

We now prove the following

THEOREM III. *For a given pair of values of t and θ, not zero, the point Q lies on line $y = x\,[\tan(t + 1)\theta]$ if and only if $t = 1$.*

PROOF: Directly substituting ξ and η from equations (3) for x and y in the equation stated in the theorem, making use of the formula for the tangent of the sum of two angles, *and clearing* of fractions, we obtain

$$(t - 1)\sec\theta\tan\theta\sec(t\theta) = 0.$$

This equation is satisfied if and only if $t = 1$, provided $\theta \neq 0$.

It is interesting to see where Q is situated in general with respect to this line $y = x[\tan(t + 1)\theta]$, since Q lies on it if and only if $t = 1$. Let φ denote the inclination of the line through the origin and Q with respect to the x-axis. Let χ denote the inclination of the line determined by the origin and the corresponding point V. We now prove the following

LEMMA. *If $0 \leqq \theta \leqq \frac{\pi}{2}$, $t > 0$, then $0 \leqq \varphi - \chi \leqq \frac{\pi}{2}$.*

PROOF: That $\varphi - \chi \leqq \frac{\pi}{2}$ follows immediately from the fact that Q and V are the extremities of a diameter of a circle passing through P and $\bar{P}$, since the vertex of the angle $\varphi - \chi$, i.e., the origin, is never interior to the circle. Now, it is clear that

$$\tan\varphi = \frac{\eta}{\xi} = \frac{\frac{a}{t}\sec\theta[\tan\theta\cos(t\theta) + t\sin(t\theta)]}{\frac{a}{t}\sec\theta[t\cos(t\theta) - \tan\theta\sin(t\theta)]},$$

which reduces to

$$\tan \varphi = \frac{\tan \theta + t \tan(t\theta)}{t - \tan \theta \tan (t\theta)};$$

and

$$\tan \chi = \frac{a[\sec \theta \sin (t\theta) - t \sin \theta \cos (t\theta)]}{a[\sec \theta \cos (t\theta) + t \sin \theta \sin (t\theta))}$$

$$= \frac{2 \tan (t\theta) - t \sin 2\theta}{2 + t \sin 2\theta \tan (t\theta)}.$$

Using these results, one readily finds that

$$\tan (\varphi - \chi) = \frac{2 \tan \theta + t^2 \sin 2\theta}{2t - t \sin 2\theta \tan \theta}.$$

The numerator of this expression is certainly not negative if $0 \leqq \theta \leqq \frac{\pi}{2}$. For all positive values of t the denominator is not negative; because, if $\sin 2\theta$ be replaced by $2 \sin \theta \cos \theta$, the denominator may be written as

$$2t(1 - \sin^2 \theta) = 2t \cos^2 \theta \geqq 0.$$

It follows, therefore, that $\tan (\varphi - \chi) \geqq 0$; hence $0 \leqq \varphi - \chi \leqq \frac{\pi}{2}$, if $0 \leqq \theta \leqq \frac{\pi}{2}$. This proves the lemma.

We now prove the following

THEOREM IV. *If* $0 < \theta < \frac{\pi}{2}$, $t > 0$, *it follows that* $(t + 1)\theta \gtreqless \varphi$ *according as* $t \gtreqless 1$; *while for any* t, $\lim_{\theta \to \pi/2} [(t + 1)\theta - \varphi] = 0$.

PROOF: Since Q and V lie on opposite sides of the chord $P\overline{P}$ for all θ such that $0 < \theta < \frac{\pi}{2}$, it follows from the lemma that $\chi < t\theta < \varphi$, from which it is easily shown that $(t + 1)\theta - \varphi \leqq \frac{\pi}{2}$. Now,

$$\tan [(t + 1)\theta - \varphi] = \frac{\tan [(t + 1)\theta] - \tan \varphi}{1 + \tan [(t + 1)\theta] \tan \varphi}$$

$$= \frac{\dfrac{\tan (t\theta) + \tan \theta}{1 - \tan (t\theta) \tan \theta} - \dfrac{\tan \theta + t \tan (t\theta)}{t - \tan \theta \tan (t\theta)}}{1 + \dfrac{\tan (t\theta) + \tan \theta}{1 - \tan (t\theta) \tan \theta} \cdot \dfrac{\tan \theta + t \tan (t\theta)}{t - \tan \theta \tan (t\theta)}}$$

$$= \frac{(t - 1) \tan \theta \sec^2 (t\theta)}{(t + \tan^2 \theta) \sec^2 (t\theta)} = \frac{t - 1}{t \cot \theta + \tan \theta}.$$

This expression agrees with $t - 1$ in algebraic sign. Finally, for a given value

of t, the limit approached as $\theta \to \frac{\pi}{2}$ is zero. This completes the proof.

It has just been shown that $\lim_{\theta \to \pi/2} \varphi = (t+1)\frac{\pi}{2}$, if $t > 0$. Now, draw a line through the origin inclined at an angle $(t+1)\theta$ with respect to the x-axis. Choose two points, R and S, on this line such that line segment $OR = \bar{\rho} \sec \theta$, and segment $OS = \rho \sec \theta$, where O denotes the origin. The following theorem is true:

THEOREM V.

$$\operatorname*{Lim}_{\theta \to \pi/2} \frac{OR + OS}{2\,OQ} = t\,, \textit{ provided } t \neq 0.$$

PROOF:

$\frac{OR + OS}{2} = \frac{\bar{\rho} + \rho}{2} \sec \theta = a \sec^2 \theta$, while line segment OQ

$$= \frac{a}{t} \sec \theta \sqrt{t^2 + \tan^2 \theta}.$$

Therefore,

$$\lim_{\theta \to (\pi/2)} \frac{OR + OS}{2OQ} = \lim_{\theta \to (\pi/2)} \frac{t \sec \theta}{\sqrt{t^2 + \tan^2 \theta}} = \lim_{\theta \to (\pi/2)} \frac{t}{\sqrt{t^2 \cos^2 \theta + \sin^2 \theta}} = t.$$

COROLLARY III. *When $t = 1$, Q bisects line segment RS.*

4. *Behavior of λ_t, Γ_t and Ω_t for certain limiting values of θ.* It has already been noted that every λ_t curve passes through the point $(a, 0)$. This is also true concerning the Γ_t and the Ω_t curves, as is readily seen from equations (2) and (3) when $\theta = 0$, except that Ω_t does not exist when $t = 0$.

The behavior of λ_t and Γ_t as $\theta \to \pm \frac{\pi}{2}$ is more interesting. Because of symmetry, it is sufficient to consider when $\theta \to \frac{\pi}{2}$. Since

$$\lim_{\theta \to (\pi/2)} \bar{\rho} = a \lim_{\theta \to (\pi/2)} \frac{1 - \sin \theta}{\cos \theta} = \lim_{\theta \to (\pi/2)} \frac{-\cos \theta}{-\sin \theta} = 0,$$

point $\bar{P}$ approaches the origin. Since $\lim_{\theta \to \pi/2} \rho = \infty$, point P tends toward infinity. Moreover, since

$$\lim_{\theta \to (\pi/2)} \frac{dy}{dx} = \lim_{\theta \to (\pi/2)} \frac{t + \sec \theta \tan (t\theta)}{\sec \theta - t \tan (t\theta)} = \lim_{\theta \to (\pi/2)} \frac{t \cos \theta + \tan (t\theta)}{1 - \cos \theta \tan (t\theta)} = \tan \frac{\pi t}{2},$$

provided t is not an odd integer, the equation of the asymptote to λ_t is

$$\left(\sin \frac{\pi t}{2}\right) x - \left(\cos \frac{\pi t}{2}\right) y + c = 0,$$

where c is to be so determined that the numerical distance between the λ_t curve and this line tends to zero as $\theta \to \frac{\pi}{2}$. Putting the equation in normal form and substituting for x and y the values given in (1′), we express this distance as

$$d = \frac{a\,(\sec\theta + \tan\theta)\left[\sin\frac{\pi t}{2}\cos(t\theta) - \cos\frac{\pi t}{2}\sin(t\theta)\right] + c}{\sqrt{\sin^2\frac{\pi t}{2} + \cos^2\frac{\pi t}{2}}},$$

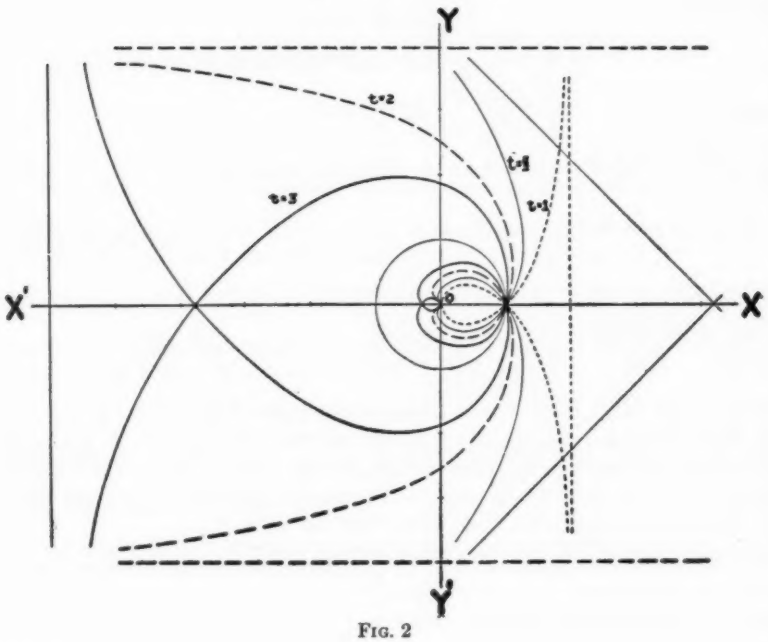

FIG. 2

which becomes

$$d = a\,(\sec\theta + \tan\theta)\sin\left(\frac{\pi t}{2} - t\theta\right) + c.$$

We now require $d \to 0$ as $\theta \to \frac{\pi}{2}$, and put

$$c = a \lim_{\theta\to(\pi/2)}\left\{\frac{(1+\sin\theta)\sin\left[t\left(\theta-\frac{\pi}{2}\right)\right]}{\cos\theta}\right\}$$

$$= a \lim_{\theta\to(\pi/2)}\left\{\frac{\cos\theta\sin\left[t\left(\theta-\frac{\pi}{2}\right)\right] + t\,(1+\sin\theta)\cos\left[t\left(\theta-\frac{\pi}{2}\right)\right]}{-\sin\theta}\right\}$$

$$= -2at.$$

It follows from symmetry that c becomes $2at$ as $\theta \to -\frac{\pi}{2}$. Thus the asymptotes to λ_t are

$$y = \pm \left(\tan \frac{\pi t}{2}\right) x \mp 2at \sec \frac{\pi t}{2},$$

the upper signs holding when $\theta \to \frac{\pi}{2}$, the lower signs, when $\theta \to -\frac{\pi}{2}$.

A like procedure leads to exactly the same equations as asymptotes to the corresponding Γ_t curve.

Horizontal and vertical asymptotes are obtained when t is an even and an odd integer, respectively.

Figure 2 shows the λ_t curves, with asymptotes, for the special cases $t = 1$, $\frac{3}{2}$, 2, and 3.

STUDIES IN THE LEGUMINOSAE

IV Chromosome Numbers and Geographical Relationships of Miscellaneous Leguminosae

By Earlene Atchison

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The general stability of chromosome number in the Leguminosae has been studied on the specific, generic, and tribal levels by Senn (1938) and Atchison (1947a, 1947b, unpublished). This list of chromosome numbers is intended as a supplement to the data obtained by Senn on mostly temperate members of the family, which the author will later compare with data on the tropical groups.

Material for cytological study of 28 species was grown in the field and greenhouse at the Blandy Experimental Farm from seed or plants obtained from botanical gardens and collectors, or collected in the field by the author. All counts were made from acetic orcein leaf smears with the exception of *Ormosia panamensis*, which was studied from Feulgen root-tip sections. Leaves of the *Gleditsia* species were pretreated for one hour with a saturated aqueous solution of paradichlorobenzene. Drawings (Figs. 1–27) were made at a camera lucida magnification of approximately 5000 and reduced in reproduction to approximately 2500. Species name, source of material, general distribution and $2n$ chromosome number are included in Table 1.

None of the chromosome counts, with the exception of *Gleditsia amorphoides* (Castronova, 1945), has been reported previously.

Various attempts have been made to correlate polyploidy within plant groups with climatic distribution. Hagerup (1932), and others found a positive correlation between northern distribution and polyploidy; Bowden (1940) found polyploids generally no more resistant to cold than diploids. Senn (1938) could not demonstrate a correlation of polyploidy with a wider or more northerly distribution in the Leguminosae. Because of the difficulty in determining the chromosome number level at which diploidy ceases and polyploidy begins, and because of the unavoidable variation in taxonomic species concepts among unrelated plant groups, it is difficult to interpret the climatic or geographical distribution of chromosome variations without special attention to the nature of the individual species.

Schrankia angustata is a shrubby briar of southeastern North America; *Calliandra inaequilatera* is a shrub from Bolivia. Although *S. angustata* is warm temperate and *C. inaequilatera* is tropical both have $2n = 16$ chromosomes, while the majority of the Mimosoideae are warm temperate or tropical, with $2n = 26$ chromosomes.

Among the Caesalpinioideae the woody temperate genera *Cercis*, *Gymno-*

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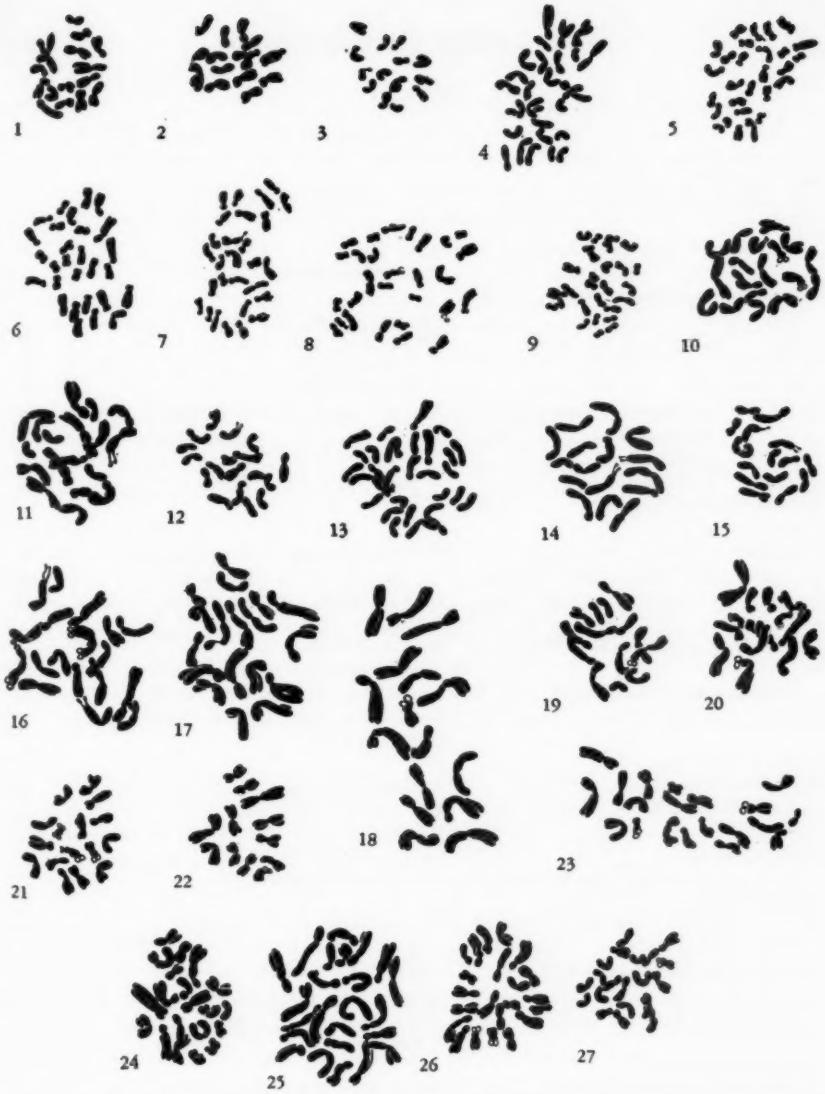

FIGS. 1–27. Chromosomes of miscellaneous Leguminosae. 1. *Schrankia angustata*, $2n = 16$. 2. *Calliandra inaequilatera*, $2n = 16$. 3. *Cercis occidentalis*, $2n = 14$. 4. *Gymnocladus dioica*, $2n = 28$. 5. *Gleditsia aquatica*, $2n = 28$. 6. *G. amorphoides*, $2n = 28$. 7. *G. heterophylla*, $2n = 28$. 8. *G. horrida*, $2n = 28$. 9. *G. sinensis*, $2n = 28$. 10. *Sophora tetraptera*, $2n = 18$. 11. *S. microphylla*, $2n = 18$. 12. *S. secundiflora*, $2n = 18$. 13. *Cladastris lutea*, $2n = 28$. 14. *Ormosia panamensis*, $2n = 16$. 15. *O. Krugii*, $2n = 16$. 16. *Podalyria australis*, $2n = 18$. 17. *Baptisia leucantha*, $2n = 18$. 18. *Caragana* sp. (*Boisseana?*), $2n = 16$. 19. *Dalea alopecuroides*, $2n = 14$. 20. *D. occidentalis*, $2n = 14$. 21. *Halimodendron argenteum*, $2n = 16$. 22. *Sesbania macrocarpa*, $2n = 12$. 23. *Stylosanthes riparia*, $2n = 20$. 24. *Zornia bracteata*, $2n = 20$. 25. *Coronilla glauca*, $2n = 24$. 26. *Rhynchosia erecta*, $2n = 22$. 27. *Galactia volubilis*, $2n = 20$.

TABLE 1

SPECIES	SOURCE OF MATERIAL	DISTRIBUTION	2n
Subfamily Mimosoideae			
Schrankia angustata T. & G.	E. A.: Garner, N. C.	East. N. Am.	16
Calliandra inaequilatera Rusby	O. E. White: Huachi, Bolivia	Bolivia	16
Subfamily Caesalpinioideae			
Cercis occidentalis Torr.	Coimbra, Portugal	Sw. N. Am.	14
Gymnocladus dioica (L.) Koch	Blandy Exp. Farm	N. Am.	28
Gleditsia aquatica Marsh.	G. T. Ratcliffe: La. P. Tabor: Ga.	S. N. Am.	28
" *amorphoides* (Gris.) Taub.	Blandy Exp. Farm	Argentina	28
" *horrida* Willd.	" " "	China, Japan	28
" *sinensis* Lam.	" " "	China	28
" *heterophylla* Bge.	" " "	China	28
Subfamily Papilionatae			
Tribe Sophoreae			
Sophora tetraptera Ait.	Coimbra, Portugal	New Zealand	18
" *microphylla* Ait.	" "	Chile, Peru	18
" *secundiflora* (Ortega) Lag.	B. A. Krukoff: Mex.	Cent. Am., S. Am., Sw. N. Am.	18
Cladastris lutea (Michx.) Koch	E. A.: Charlottesville, Virginia	N. Am.	28
Ormosia panamensis Benth.	Canal Zone	Cent. Am.	16
" *Krugii* Urb.	L. F. Holdridge: Puerto Rico	West Indies	16
Tribe Podalyrieae			
Podalyria australis	Coimbra, Portugal	S. Africa	18
Baptisia leucantha T. & B.	O. E. White: Albany, Ga.	Se. N. Am.	18
Tribe Galegeae			
Caragana sp. (Rec'd. as *Boisseana*)	Coimbra, Portugal	Asia	16
Dalea alopecuroides Willd.	" "	E. N. Am.	14
" *occidentalis* Riley	H. S. Gentry: Mex.	C. Am.	14
Halimodendron argenteum (Lam.) D. C.	Blandy Exp. Farm	E. Asia	16
Sesbania macrocarpa Muhl.	O. E. White: Brunswick, Ga.	Se. N. Am.	12
Tribe Hedysareae			
Stylosanthes riparia Kearney	E. A.: Fort Valley, Va.	E. N. Am.	20
Zornia bracteata (Walt.) Gmel.	E. A.: Garner, N. C.	Se. N. Am.	20
Coronilla glauca L.	Coimbra, Portugal	S. Europe	24
Tribe Phaseoleae			
Rhynchosia erecta (Walt.) D. C.	E. A.: Keysville, Va.	E. N. Am.	22
Galactia volubilis (L.) Britton	J. T. Baldwin: N. C.	E. N. Am.	20
Apios tuberosa Moench	Blandy Exp. Farm	E. N. Am.	ca. 40

cladus, and *Gleditsia* contain both diploids and evolutionary polyploids, *Cercis* having $2n = 14$ chromosomes and the others, $2n = 28$.

In the subfamily Papilionatae, tribe Sophoreae, *Cladastris lutea* is probably the hardiest of the species studied. The polyploid number $2n = 28$ has only been found in one other species of the tribe, *Sophora japonica*, which is also of cool temperate distribution.

The tribes Galegeae and Hedysareae present an aneuploid range of chromosome numbers and considerable variation in chromosome structure. *Caragana* sp. from southern Asia and *Halimodendron argenteum* from the salt steppes of Asia are woody, while the *Dalea* and *Sesbania* species are herbaceous or facultatively woody. The Galegeae in general are taxonomically a more heterogenous group than the Sophoreae. The diverse chromosome numbers probably represent other evolutionary specializations than climatic selection.

Three herbaceous perennials in the Phaseoleae, *Rhynchosia*, *Galactia*, *Apios*, occupy similar areas in eastern North America. *R. erecta* and *G. volubilis* have $2n = 20$, *A. tuberosa*, $2n =$ ca. 40.

There is no evidence from the present data to support either positive or negative correlation of chromosome number with climatic distribution. Among the legumes considered here, both diploids and polyploids are found in tropical as well as temperate areas. White (1926, 1940) expressed the idea that in any plant population mutations for temperature tolerance may occur at random regardless of geographical distribution. Survival through hardiness seems to be more frequently a gene character which may find expression in either diploid or polyploid than a direct result of polyploidy.

There are approximately 6 species of trees and shrubs bearing polygamous flowers in *Gleditsia* (Burkhart, 1943). Geological evidence of the origin of the genus is meager, although Berry (1923) states that "a genus called *Gleditsiophyllum* found in both the Upper Cretaceous and the Eocene of North America is suggestively like the honey locust." Antiquity of origin is further supported by the presence of species of extreme morphological similarity in the temperate zones of North America and Asia as well as South America and Africa. Castronova (1945) has previously reported $2n = 28$ chromosomes in *G. amorphoides*, indigenous to Argentina. Atchison (1947a) reported $2n = 28$ in 33 collections of *G. triacanthos*, the North American honey locust; these represent a fair sampling of its range. In relation to other representatives of the Caesalpinioideae, i.e., *Cercis*, $2n = 14$, all present day Gleditsias which have been studied cytologically are polyploid. Little variation in chromosome size and structure can be noted among the species, though they have long been geographically separated. It may be assumed that chromosome variants including ancestral species with a lower number, if such have occurred, did not have sufficient survival value to withstand the climatic changes of the ages. The similar polyploid character and lack of specific morphological variation among the discontinuously distributed species of *Gleditsia* support its position as a relic genus of ancient origin and emphasize the chromosomal stability of the woody genera of the Leguminosae.

SUMMARY

Chromosome numbers are reported for 28 species of Leguminosae, including 9 species native to North Carolina. Comparisons of diploid and polyploid distributions show no correlation between temperature tolerance and polyploidy. The similarity of chromosome number and morphology among 6 discontinuously distributed species of *Gleditsia* supports the interpretation of the genus as a group of closely related relics of common origin.

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LENGTH OF APPLICATION OF THE EXCYSTMENT-INDUCING STIMULUS IN RELATION TO PERCENTAGE OF EXCYSTMENT IN TILLINA MAGNA[1]

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INTRODUCTION

It is well known that various types of environmental changes are effective in inducing the emergence of ciliated protozoa from their resting cysts. However, it is difficult to generalize with reference to the effectiveness of such changes in that a change which is effective for the cysts of one kind of ciliate may be ineffective for those of another. Dried cysts are excluded from consideration in the present study; all references to cysts therefore concern wet cysts; i.e., those immersed in a fluid medium. Plant extracts seem to be the most generally effective excystment-inducing substances. Thus, Barker and Taylor (1933) regularly excysted *Colpoda cucullus* with alfalfa infusion and yeast autolysate. Thimann and Barker (1934), noting that timothy hay infusion was highly effective for *Colpoda cucullus*, undertook an analysis of hay infusion in an effort to isolate and identify the effective substances. Haagen-Smit and Thimann (1938) continued the analysis and concluded that the effective substances were the plant acids and the sugars.

However, not all ciliate cysts require plant infusions or other types of organic substances for their excystment. Thus, Garnjobst (1928, 1937) could induce excystment in the hypotrichs *Euplotes taylori* and *Stylonethes sterkii* merely by diluting the original encystment medium with distilled water, and Beers (1945) found that distilled water alone was highly effective in excysting *Tillina magna*. Johnson and Evans (1940) distinguished two types of resting cysts in *Woodruffia metabolica*, "stable" cysts requiring organic substances and "unstable" cysts not requiring organic substances. Strickland and Haagen-Smit (1947, 1948) found that certain concentrations of potassium phosphate are effective excysting agents for *Colpoda duodenaria*.

The cysts of some ciliates appear to be very highly specialized with reference to their requirements for excystment. For example, Weyer (1930) found that bacterized gelatin solutions were the most effective agents in excysting *Gastrostyla steinii* after distilled water and inorganic media failed. Beers (1946) induced excystment in *Didinium nasutum* by using bacterized plant infusions after distilled water and other media failed.

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The cysts of *Tillina magna*, on the contrary, respond to a wide variety of environmental changes. Thus, Beers (1945) was able to induce excystment by means of distilled water, which had a high degree of excystment-inducing activity, and various plant infusions. A 0.05 per cent lettuce infusion was found to be the most effective excysting stimulus. In general, the results furnished by the studies of Beers (1945) and Bridgman (1948) indicate that the primary excystment-inducing factor in *Tillina* is of an osmotic nature, involving the entrance of water into the cell. The fact that cysts become active more rapidly in certain concentrations of lettuce and other plant infusions than in distilled water (Beers, 1945) indicates that the infusions contain specific excystment-inducing substances (the sugars and certain salts of the plant acids) which intensify the effects of the osmotic factor.

Although numbers of investigators have occupied themselves with the identification of some of the factors which are responsible for excystment, only Weyer seems to have given special consideration to the relationship which may exist between the length of the period of immersion in the excystment-inducing medium and the percentage of excystment. Weyer found that in *Gastrostyla steinii* the excystment-inducing medium must act continuously on the cysts throughout the entire process of differentiation and emergence. Otherwise, the process of differentiation and emergence ends, and the organisms return to the resting condition.

The relative ease and dependability with which the wet cysts of *Tillina magna* can be activated suggested the use of this ciliate in a further study of the effects of interrupting the excystment process. In considering this problem the following questions arise: What is the effect of transferring excysting specimens of *Tillina magna* from the excystment medium back to the original encystment medium? Is the process of excystment actually interrupted, as in *Gastrostyla*, with subsequent dedifferentiation and return to the encysted stage? Or is the process irreversible, once it is well under way? Is there a critical or threshold condition beyond which re-encystment is impossible, or can re-encystment be induced at any stage of the excystment process by discontinuing the application of the excysting stimulus? Thus, the present study concerns the relation of the length of application of the excysting stimulus to the subsequent events of the excystment process. Considered from the standpoint of experimental practicability, it concerns the relation between the length of application of the excysting stimulus and the percentage of individuals that excyst upon return to the original encystment medium.

MATERIAL AND METHODS

The tillinas used in this study were cultured in a 0.05 per cent lettuce infusion with the bacterium *Aerobacter aerogenes* used for food. The lettuce infusion was prepared by boiling 0.05 gm. of powdered dried lettuce in 100 cc. of Pyrex-distilled water for 5 minutes. This was then filtered and distributed to 30-cc. test tubes, each tube one-half to two-thirds full. Cotton plugs were inserted into each tube, and the lettuce infusion was then autoclaved. *Aerobacter* was cultured in Petri dishes on Difco nutrient agar.

In preparing *Tillina* cultures for the production of cysts, the following method was used: One cubic centimeter of 0.05 per cent lettuce infusion was put into a Columbia culture dish. Twenty-four active tillinas, all of the same clone, were put into the dish. Then with a small, sterile pipette 5–6 drops of a concentrated suspension of bacteria and lettuce infusion were added to the dish containing the active tillinas. This suspension was made by stirring 7–8 loops of bacteria into 1 cc. of lettuce infusion. Eight or ten of these cultures were usually begun at one time, and a stock culture was maintained to supply specimens for future use. The cultures were kept in a moist chamber with the temperature at 22–23°C.

Tillina magna multiplies rapidly as long as sufficient quantities of food are present. As the food supply became diminished in the cultures mentioned above, the animals began to swim about actively and very soon encysted. The ciliates usually began to encyst on the third day after the beginning of a culture, and by the end of the third day practically all the tillinas had encysted. At this time a great number of individuals had been formed, so that the number of cysts present was easily 350. The cysts used in the experiments were all of one clone. The cyst preparations were, then, completion cultures, prepared as needed. After all the animals in a dish had encysted, the cysts were allowed to remain for 4 more days during which time they reached a state of maturity or physiological stability. They were then ready for experimental use.

Attempts to culture *Tillina* on a strain of *Pseudomonas fluorescens* obtained from the Department of Bacteriology, School of Medicine, University of North Carolina, were unsuccessful, although Beers (1945) used a different strain of *Pseudomonas* with complete success. A strain of *Aerobacter aerogenes*, also obtained from the same source, was then tried and proved satisfactory. Kidder (1941) pointed out that *Tillina canalifera* is extremely selective in its choice of food, and in one experiment thrived on only one of 26 kinds of bacteria which were isolated from a wild culture of this ciliate. Apparently *T. magna* is equally selective, and this marked selectivity is probably the factor which accounts for the seeming rarity of *Tillina* in nature.

As already stated, Columbia culture dishes were used for obtaining the cyst preparations. There was a specific reason for using this type of dish. Boveri dishes were first employed in obtaining resting cysts of *Tillina*. However, when cysts were detached from their positions on the sides of the dish just beneath the surface of the encystment medium and allowed to fall to the bottom, it was found that in a short time excystment occurred in many of the cysts. It was conjectured, then, that *Tillina* cysts are so sensitive to environmental changes and excyst so readily that a change from the superficial layer of fluid to the lower layer of fluid was adequate to excyst them, different conditions, such as amount of oxygen, undoubtedly being encountered. The Columbia culture dishes were therefore used in place of the Boveri dishes, since it was assumed that conditions in the shallower dishes were more uniform.

A balanced salt medium (0.012 per cent Osterhout's solution) was first used in the preparation of cysts, but in all the experiments reported in this paper 0.05 per cent lettuce infusion was used. This medium was used rather than a bal-

anced salt medium, since it has not been conclusively demonstrated that inorganic salt media are entirely favorable for *Tillina*. Lettuce infusion, on the other hand, is entirely favorable in tonicity and reaction.

The tillinas were cultured for 7–10 days before using them in the preparation of the completion cultures. This practice resulted in the formation of satisfactory stable cysts. Unless the tillinas are allowed to pass through a number of divisions prior to the production of cysts, the resulting cysts exhibit spontaneous excystment and re-encystment and are therefore unsuited for experimental use. Consequently, it should be pointed out that it is very important to culture *Tillina* for 7–10 days (15–25 generations) before attempting to get cysts.

The excystment experiments were carried out in the following manner: With a clean needle cysts were detached from the sides of a dish in groups of 5–7. (When the ciliates encyst, they tend to do so in clumps.) A total of approximately 120 cysts were transferred in a sterile pipette to a Columbia culture dish containing 1 cc. of 0.05 per cent lettuce infusion. The cysts were here washed with a stream of the fluid from the pipette. In this fresh lettuce infusion the cysts were allowed to remain for 30 minutes, for example. They were next transferred to one of the concavities of a depression slide which contained 0.2 cc. of the old lettuce infusion (original encystment medium). Here they were thoroughly washed to remove any of the excystment medium which might have remained. Upon completion of this step the 120 cysts were transferred in groups of 40 to three depressions, each containing 0.2 cc. of the old lettuce infusion. At the end of 3 hours, i.e., counting from the time the cysts were put into the excystment medium, the depressions were examined under the binocular and a record made of the number excysted in each depression. At the end of the fourth hour a second record was made. At the temperature of the experiments the tillinas usually excysted during the last half of the second hour and the first half of the third hour. Hence, records made at the end of the third hour accounted for most of the cases of excystment. Individuals that lagged were usually accounted for in the 4-hour recording, preliminary experiments having shown that if the cysts are normal and possess the potentialities of excysting, they will most certainly have excysted by the end of the fourth hour. Therefore, no additional records were made after the fourth hour. Other groups of 120 cysts were used in the same manner as that described above, allowing them to remain in the excystment medium for 1 hour, 1.5 hours, and 2 hours.

It was the practice to test 1080 cysts in groups of 120 (from separate dishes) for each of the different exposure lengths. Therefore, data were obtained on a fairly large number of cysts for each length of exposure to the excysting stimulus. The following additional information should be given: The temperature at which the experiments were performed was 22–23°C., and the experimental dishes were kept in moist chambers. Initially sterile pipettes, glassware, and media were used. The cysts were transferred to the various dishes and depressions with a minimum amount of fluid. Experiments were terminated at the end of 4 hours, since it was felt that all the cysts which were going to excyst would have done so by this time.

For control purposes when running an experiment, cysts were subjected to the usual experimental manipulations, but with old lettuce infusion from a completion culture substituted for fresh lettuce infusion. These cysts showed no activity whatsoever. Thus, the mechanical operations of the experimental procedure are in themselves without effect on the cysts. As a means of testing the viability of the cysts in an experiment, some were transferred in groups of 20 to 0.2-cc. amounts of fresh 0.05 per cent lettuce infusion and left in it. These always excysted, yielding practically 100 per cent emergence.

Worthy of mention are some facts regarding the use of lettuce infusion as the excysting agent. The old lettuce infusion of the completion cultures is acted on by bacteria and contains waste products of bacterial and *Tillina* metabolism. The accumulation of this material in the medium and the accompanying depletion of the original nutrient materials evidently results in a condition of equilibrium between cysts and surrounding medium such that excystment does not occur spontaneously. Fresh, sterile 0.05 per cent lettuce infusion, not having been acted on by bacteria and containing none of the waste products of bacterial and *Tillina* metabolism, is therefore very different from the old lettuce infusion and is a highly effective excystment medium. The cysts, upon transfer to this medium, encounter a change of environment, with subsequent entrance of water into the protoplasts and eventual excystment.

For each exposure length the total percentage of cysts that excysted 3 hours and 4 hours after application of the excysting stimulus was calculated. For example, with reference to the cysts exposed 0.5 hour, the numbers of specimens excysted at the end of 3 hours in each of the three depressions of a group of 120 were added, the same being done for the other groups of 120. Then these sums—nine in all—were added, giving the total number excysted at the end of 3 hours. This number was converted to a percentage. In like manner, the percentage of excystment at the end of 4 hours was calculated. For the other exposure lengths—1 hour, 1.5 hours, and 2 hours—the same procedure was followed.

RESULTS OF EXPERIMENTS

The experimental results are summarized in accompanying Table 1.

A total of 1080 cysts were exposed to the excysting stimulus (0.05 per cent fresh lettuce infusion) for 0.5 hour and were then returned to the original encystment medium. Only 1.3 per cent of them excysted. There is no doubt that these cysts were affected slightly by the presence of the excysting stimulus, since they showed, as Table 1 indicates, moderate cyclosis at the time of removal from the excystment medium. Many of these cysts, as well as those used in other experiments, were examined under the compound microscope just before immersion in the excystment medium; very few of them showed cyclosis at this time. It is evident from these results that application of the excysting stimulus for only 0.5 hour, though adequate to induce cyclosis, is inadequate to cause any appreciable number to excyst when returned to the encystment medium.

A like number of cysts (1080) were exposed to the excysting stimulus for 1 hour (Table 1) before being returned to the original encystment medium.

These cysts, after 1 hour in fresh lettuce infusion, contained numerous vacuoles in the cytoplasm, showing that water had entered the cysts in appreciable quantities, and they were usually ciliated and rotating slowly in their membranes. Upon return to the encystment medium 83.5 per cent of them had excysted at the end of 3 hours, counting from the time when the excysting stimulus was first applied. At the end of the fourth hour an additional 1 per cent had excysted, giving a total of 84.5 per cent. In comparing these results with those involving a half-hour exposure, it is seen that a one-hour exposure produces an enormous increase in the percentage of excystment.

Then, a total of 1080 cysts were exposed 1.5 hours to the action of the excystment medium before being returned to the original encystment fluid. At the time of their return about half of the total number had escaped from the ectocyst

TABLE 1

Tillina magna. Relation between length of exposure to excystment-inducing stimulus and percentage of excystment upon return to original encystment medium. Temperature: 22–23°C.

TOTAL NUMBER OF CYSTS TESTED	LENGTH OF EXPOSURE TO EXCYSTING STIMULUS	CONDITION OF CYSTS WHEN REMOVED FROM EXCYSTMENT MEDIUM	EXCYSTED AT END OF 3 HOURS, COUNTING FROM BEGINNING	EXCYSTED AT END OF 4 HOURS, COUNTING FROM BEGINNING
	hours		*per cent*	*per cent*
1080	0.5	Cyclosis only.	1.3	1.3
1080	1	Numerous vacuoles; usually ciliated and rotating slowly; membranes intact.	83.5	84.5
1080	1.5	Some free in endocyst; others still vacuolated and rotating in unruptured membranes.	87.5	88.4
1080	2	Practically all now excysted.	98.5	98.5

and mesocyst and were imprisoned only in the endocyst, while the others were still vacuolated and rotating inside the unruptured membranes. Hence, none of them qualified as wholly excysted at the time of their return. However, 87.5 per cent of these cysts had excysted when the 3-hour readings were made, and 88.4 per cent an hour later.

Finally, 1080 cysts were exposed to the excystment medium for 2 hours. This length of exposure at 22–23°C. was adequate to induce the excystment of practically all of them, so that only a small fraction of the original 1080 could be returned to the encystment fluid. These continued their differentiation, with the result that 98.5 per cent of the cysts of this group excysted.

DISCUSSION

From the foregoing results it is seen that the cysts of *Tillina magna* differ from those of *Gastrostyla steinii* in their response to an interruption of the excystment-

inducing stimulus. Whereas the cysts of *Gastrostyla*, according to Weyer, require the continuous presence of the excystment medium in order to complete their emergence, those of *Tillina* continue the process of differentiation and emergence when they are removed from the excystment medium and returned to the old encystment medium. However, the excystment medium must be allowed to act long enough on the cysts of *Tillina* to set forcibly in motion the sequence of changes in the excystment process. Once these changes are well under way, the process of excystment is irreversible.

The induction of cyclosis by means of a half-hour immersion in the excystment medium does not suffice to stimulate the cysts to complete the excystment process; upon return to the encystment medium the process of excystment, of which cyclosis is the initial manifestation, ceases in practically all such cysts. If the immersion in the excystment medium is lengthened to an hour, nearly 85 per cent of the cysts become active upon return to the old medium. These cysts, after an hour's immersion, contain numerous vacuoles, showing that water has entered the cytoplasm in appreciable quantities; and they are usually rotating slowly in their membranes, as has been said, showing that the cilia are sufficiently developed to be weakly functional. This stage of excystment appears to constitute a critical or threshold condition. If this condition is not attained, the process of excystment is discontinued upon transfer to old medium. If this condition is actually attained, the process of excystment goes to completion, regardless of the subsequent presence of the excystment medium.

Since an immersion of 1 hour in the excystment medium at 22–23°C. is sufficient to induce the emergence of approximately 85 per cent of the cysts, it follows logically that an immersion of 1.5 hours should induce a still higher percentage of excystment. Thus, 88.4 per cent of such cysts emerged in the experiments. An immersion of 2 hours at the temperature of the experiments is in itself sufficiently long to induce the emergence of practically all the cysts, so that the return of the few still unexcysted specimens of this group to encystment medium was always without effect on their emergence.

SUMMARY

1. Resting cysts of *Tillina magna* were obtained in Columbia culture dishes containing 0.05 per cent lettuce infusion to which *Aerobacter aerogenes* had been added as food. These were completion cultures.

2. Cysts were transferred to the excystment medium (fresh 0.05 per cent lettuce infusion) and allowed to remain for 0.5 hour, 1 hour, 1.5 hours, or 2 hours before return to the encystment medium. A total of 1080 cysts were tested for each of the four exposure lengths, with the temperature at 22–23°C.

3. The groups of cysts which were exposed to excystment medium for 0.5 hour, 1 hour, and 1.5 hours, and then returned to encystment medium, showed the following percentages of excystment, respectively: 1.3 per cent, 84.5 per cent, and 88.4 per cent. Cysts that were left in the excystment medium for 2 hours had practically all excysted at the end of this time. The few which had not

excysted were returned to the encystment medium, with a resulting 98.5 per cent excystment for the total number of cysts tested.

4. Once the excystment changes are well under way in the cysts, the process is irreversible. The cysts do not require the continuous presence of the excystment medium in order for excystment to occur. The results indicate that the cysts must remain in the medium until they acquire numerous vacuoles and reach a condition of rotation within the membranes. In most cysts this condition is attained after about 1 hour of immersion in the excystment medium, though the time required is variable. If this condition is actually reached, the cysts will excyst, regardless of the presence or absence of the excysting stimulus.

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A NEW SPECIES OF ANCYLISTES ON A SACCODERM DESMID

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Plates 6 and 7

The genus *Ancylistes*, now containing a small group of obligate parasites on desmids, was established by Pfitzer (1872) for a species which he found parasitizing *Closterium acerosum* at Bonn, Germany. This species, named *A. Closterii* by Pfitzer, has since been reported by several workers from Europe, Asia, and North America. Since Pfitzer's work, three additional species have been described. The first of these was described by Fritsch (1895) as *Ancylistes cladocerarum*, parasitic on rotifers, but has not been accepted by later workers as a valid species of *Ancylistes*. A year later Beck (1896) described a third species, *A. Pfeifferi*, based on material collected by Löfgren in Brazil. Beck's species was incompletely described from scanty material, and the vegetative stages were doubtless partly confused with *Myzocytium megastomum*. The discovery by Berdan (1938) of a species identical with or closely related to Beck's serves partly to validate his, and while she points out differences between the two in the size of the resting bodies and the number of protuberances on the wall she lets her parasite go under Beck's binomial *A. Pfeifferi*. A fourth species, *Ancylistes Miurii*, was described by Skvortzow (1925) in *Closterium* sp. from North Manchuria. There is some doubt as to whether this fungus belongs in *Ancylistes* or *Myzocytium*, as noted by Berdan, since the mycelium has the beaded appearance of *M. megastomum*.

At present there seem to be only two valid species of *Ancylistes*, *A. Closterii* and *A. Pfeifferi*. Both of these have been reported on species of the genus *Closterium*. It is unfortunate that not all observers have identified the species of host, indeed it seems that only Pfitzer and Berdan have done so. It is highly probable that not all of the parasites identified as *Ancylistes Closterii* belong to that species.

In Berdan's paper (1938), the most complete account of the genus so far published, she describes two species, tentatively identified as *A. Closterii* and *A. Pfeifferi*, and reports her remarkable discovery of conidia forcibly discharged into the air as in *Conidiobolus*, *Empusa*, etc., and on the basis of that discovery transfers the genus to the Entomophthorales.

As mentioned above, the authentic species of *Ancylistes* previously described have been found on species of *Closterium*, a genus of the placoderm desmids. The chief purposes of the present paper are to describe a species parasitic on a saccoderm desmid, *Netrium*, and to corroborate Berdan's discovery of conidia in *Ancylistes*.

Ancylistes Netrii n. sp.

Vegetative mycelium within the protoplast of host cell, consisting upon reaching mature size of a branched non-septate thread which usually starts its growth near the isthmus of the desmid in contact with the host nucleus and then elongates in opposite directions toward the ends of the desmid; at first non-segmented and 2.2–4.8 μ thick; when mature consisting of 3–6, usually 4, londitudinal branches which join in the isthmus of the desmid, becoming septate into numerous cells which are usually about 2–3 times as long as thick, measuring 8–15.5 $\times$ 15–30 μ; cytoplasm with numerous rounded granules and conspicuous round vacuoles; cells becoming conspicuously swollen just before and during germination. Reproduction by vegetative, asexual and sexual methods; all cells of thallus taking part in reproduction. In vegetative and asexual reproduction exit tubes are formed (one from each cell as a rule) and grow out at right angles or slightly diagonally from the parent cell and after coming in contact with the host wall swell distally to form a club-shaped structure about 2–4 μ thick at the base and 4–9 μ thick at the larger end; if submerged the exit tube, after emerging through the desmid wall, forms an external hypha 3–6.8 μ thick which grows through the water for some distance until it comes in contact with a new susceptible host cell; the protoplasm always in distal part of hypha and closed off from empty part by one or more cross walls. If the desmid is at the surface of the water the exit tubes form conidiophores, each unbranched and with a single apical spherical conidium; conidiophore stalk usually 25–100 μ long, sometimes longer, about 8 μ thick at its thickest point slightly below the conidium; conidia spherical, 16–25 μ thick, with a conical apiculus; forcibly discharged by the sudden outpushing of the apiculus; conidiophore with a distinct cone-shaped columella and quickly disintegrating after discharge of the conidia. Zygotes formed within the host, usually in a row in the center, between the several longitudinal hyphae and apparently by conjugation of two cells of opposite filaments, with the zygote in the conjugation tube; spherical or subspherical from pressure, 19–26 μ thick, the largest seen being 25 $\times$ 29.4 μ; wall about 2.5 μ thick, smooth; when mature with one large, slightly excentric shiny globule embedded in the cytoplasm.

In *Netrium digitus* on very moist earth and in shallow pools behind Dry Falls, near Highlands, N. C., July 17 and August 1, 1945; H. N. Couch, coll.

This species is easily distinguished from others by the club-shaped exit hyphae (fig. 17), the position of the zygotes in the center of the host cell and bounded laterally by the empty filaments of the parasite, the larger size of the conidia and zygotes, and finally by its occurrence in *Netrium*.

DEVELOPMENT OF ANCYLISTES NETRII

In this species, as in the two studied by Berdan, infection of new desmids may be by germ tubes which come directly from the cells of the intramatrical mycelium or by germ tubes which arise from discharged conidia. As shown by Berdan, conidia are formed only on desmids floating on or near the surface of the water. The conidiophores, on each of which is formed a single conidium, project about 20–50 μ into the air and hurl the conidia horizontally about two millimeters. Germ tubes from conidia or from the mycelium within other desmids approach an uninfected host and encircle it partly or completely, a phenomenon beautifully described by Pfitzer and others. These tubes growing

through the water in search of a host may reach a length of several hundred microns. As the tube elongates it becomes many times segmented, but all the compartments are empty of protoplasm except the distal one, as first shown by Pfitzer (1872).

When the end of the infecting hypha approaches the desmid wall, it enlarges to form an appressorium shaped like an adder's head. I have seen appressoria applied to various places on the host wall and it appears that penetration may be anywhere along the surface, although only a few penetration stages have been observed. The remains of the penetration tube are shown in fig. 9. Soon after the parasite enters it appears to be carried to the host nucleus, where it elongates to form a short tube in contact with this organ (fig. 10). Dangeard (1886) describes the young hyphae as without a definite wall in *Ancylistes Closterii*, and the same seems to be true in the present species. Dangeard also makes the interesting observation that after infection the desmid continues to move slowly by the usual tumbling movements and thus helps to bring about the distribution of the parasite.

From its central position near the nucleus the hypha branches and grows in opposite directions toward the ends of the desmid, usually with one hyphal branch in each groove between the longitudinal plates of the chloroplast (figs. 11, 12). Not infrequently when a hypha reaches the end of the desmid it grows around the end of the chloroplast and comes back on the opposite side (fig. 13), as indicated by Berdan. The mature hyphae are over twice as thick as the young threads. It appears that the increase in thickness occurs mostly after the growth in length has ceased. The septations also appear after the hypha has attained its full length. These are not formed simultaneously but progressively from one region to another (fig. 13). Material mounted in lactophenol with dilute coton blue shows that each segment contains several nuclei as do the conidia, gametangia, and zygotes, thus corroborating Dangeard's (1906) observations. The mature mycelium consists of about 30–50 multi-nucleated cells, each of which normally functions in reproduction in one of three ways: a cell may give rise to an exit tube which penetrates the desmid wall to form an external infecting hypha; it may, after forming an exit hypha, give rise to a conidiophore; or a cell may form a gametangium which fuses with another to form a zygospore or without fusion a cell may form an azygospore.

Just before the exit tubes arise, the cells swell considerably so that the hyphae appear constricted at the septa. The exit tube always rises at the end of a cell growing straight out or slightly diagonally toward the host wall (figs. 5, 17). It is a rather narrow tube and at first is of the same diameter throughout its length (fig. 14).

The cell wall of *Netrium* consists of a homogeneous inner layer of cellulose and an outer layer of pectose according to Lütkemüller (1902, from Smith, 1933). Viewed under the water immersion there usually appear to be an outer, thinner, hyaline layer and a much thicker, inner, slightly yellowish layer (fig. 18). This thicker layer seems at times to be bounded internally by a third, thinner, hyaline layer. The observations presented below seem to indicate the presence of a third inner layer.

When the exit tube touches the wall of the desmid it penetrates the inner layer of the host wall and then enlarges to form a club-shaped structure (figs. 14–16). As the end of the hypha enlarges a thin, inner part of the wall is separated off from the thick yellowish part, since it separates more easily than it tears (fig. 18). This part that separates off seems to be a true third layer. The inner wall is probably penetrated by enzymatic action of the hyphal tip, while the thicker middle and outer parts, in which valvular cracks may sometimes be observed, are apparently cracked by force. One of the best lines of evidence that mechanical force is exerted against the outer wall and that the inner wall counterbalances this force is that when the exit hypha is empty or is slightly plasmolyzed the wall of its enlarged portion, between the outer and inner walls, buckles considerably (figs. 18, 20). Similar behavior was shown by the exit hyphae of *Ancylistes Closterii*, as shown by Berdan in her fig. 4. She considered this inner layer (labelled M in her figure) as the plasma membrane but it probably was the inner wall layer. In *Ancylistes Pfeifferi* penetration by the exit tube, judging from Berdan's figs. 12 and 13, is effected in a different manner than in *A. Netrii* and *A. Closterii*. This may be due to differences in the wall structure of the host. The type of penetration shown by the latter two, in which the host actually assists the parasite in puncturing the host wall, is unreported in previous literature (see Gäumann, 1945) and should be more thoroughly studied in this genus. The germ tubes of *Ancylistes* are large and penetration can easily be observed in the living condition.

As stated above, the exit tube may, when it reaches the outside of the desmid, grow into a hypha which infects directly some other desmid. If the tube is close to the surface of the water, it may form a conidiophore (figs. 1, 17, 19). Each cell of the mycelium may give rise to a conidiophore and thus several dozen may arise from one desmid. The conidiophores are formed and forcibly discharged in this species just as in *A. Closterii* and *A. Pfeifferi*, as described by Berdan.

My observations on the conjugation of the gametangia and the formation of the zygote are inconclusive, for although I had an abundance of living material in all stages I was unable to follow the development of the zygote. My observations were made from material preserved in lactophenol and stained with coton blue. The zygotes are formed mostly by scalariform conjugation and mature in what appears to be a conjugation tube (figs. 21, 22). They are almost always in one or two irregular longitudinal rows in the center of the desmid, surrounded by the longitudinal hyphae, and hence it is quite difficult to follow the stages in their development (figs. 7, 8, 22). The germination of the zygote has not been seen.

SUMMARY

A new species of *Ancylistes* is described as *A. Netrii*. This is the first time this genus has been reported on a saccoderm desmid. Conidia are reported in this species, thus confirming Berdan's earlier discovery of conidia in two other species. The exit tube of *A. Netrii*, in making its way through the host wall,

first penetrates the inner wall layer. The end of the tube then swells, separating the inner layer from the outer and the tension set up by the stretching of the inner layer assists the fungus in pushing through the outer layer. This method of host wall penetration, found also in *A. Closterii*, seems to be unreported for any other genus.

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EXPLANATION OF PLATES 6 AND 7

Ancylistes Netrii

FIG. 1. Several conidiophores projecting from desmid up to surface of water. Some have already shot their conidia and the columellae are still visible; others have spherical conidia attached. × 270.

FIG. 2. Short conidiophore (lower part of photograph) which has just shot its conidium, and a long one with indistinct stalk and conidium still attached. This has been flooded with water and the vacuole destroyed, so the conidium will not be discharged. The irregular granular body near center is perhaps an amoeba. × 625.

FIG. 3. Mycelium mature and becoming septate but no reproduction yet. Dark material in center is disorganized chloroplasts which were still green when the photograph was made. × 270.

FIG. 4. Slightly later stage than above. × 270.

FIG. 5. Exit hyphae about to emerge through desmid wall to form conidiophores. Note how mycelium of parasite has been pushed to side of desmid. × 270.

FIG. 6. Two exit tubes which have penetrated through wall. Note host wall split. Plasma membrane is close to large parasite cells. For further explanation see text. × 625.

FIGS. 7, 8. Zygotes almost completely covered by the disorganized plastids and by the empty hyphae of parasite. In fig. 8 five zygotes can be made out indistinctly. × 385.

FIG. 9. Showing infection tube passing through host wall. × 1400.

FIG. 10. Earliest stage of parasite recognized. Hypha (h) without a cell wall is in contact with host nucleus (h. n.). × 368.

FIGS. 11, 12. Hyphae elongating. New branches forming at isthmus of desmid. × 368.

FIG. 13. Septa forming progressively. × 368.

FIGS. 14–16. Stages in exit hyphae penetrating host wall to exterior. p.m. plasma membrane; i. w. and o. w., inner and outer parts of host wall, respectively. For further explanation see text. × 1000.

FIG. 17. Desmid containing mycelium forming conidiophores, one from each hyphal segment. Such a desmid is close to the surface of the water and usually in a horizontal position. × 290.

FIG. 18. Exit hypha buckled after pushing through outer part of host wall and forming conidiophore. × 1400.

FIG. 19. Conidiophores. On left, with conidium attached; on right just after conidium has been shot from stalk. *A*, apiculus; *C*, columella; *V*, vacuole. Diagrammatic. × 290.

FIG. 20. Mycelium, every segment of which has formed a conidiophore. Only 7 exit tubes are shown. Cross-hatched material in center represents dead remains of chloroplasts. × 368.

FIG. 21. Young zygote apparently formed in conjugation tube. × 635.

FIG. 22. Two zygotes nearly mature, the lower with large excentric fat body. × 635.

PLATE 6

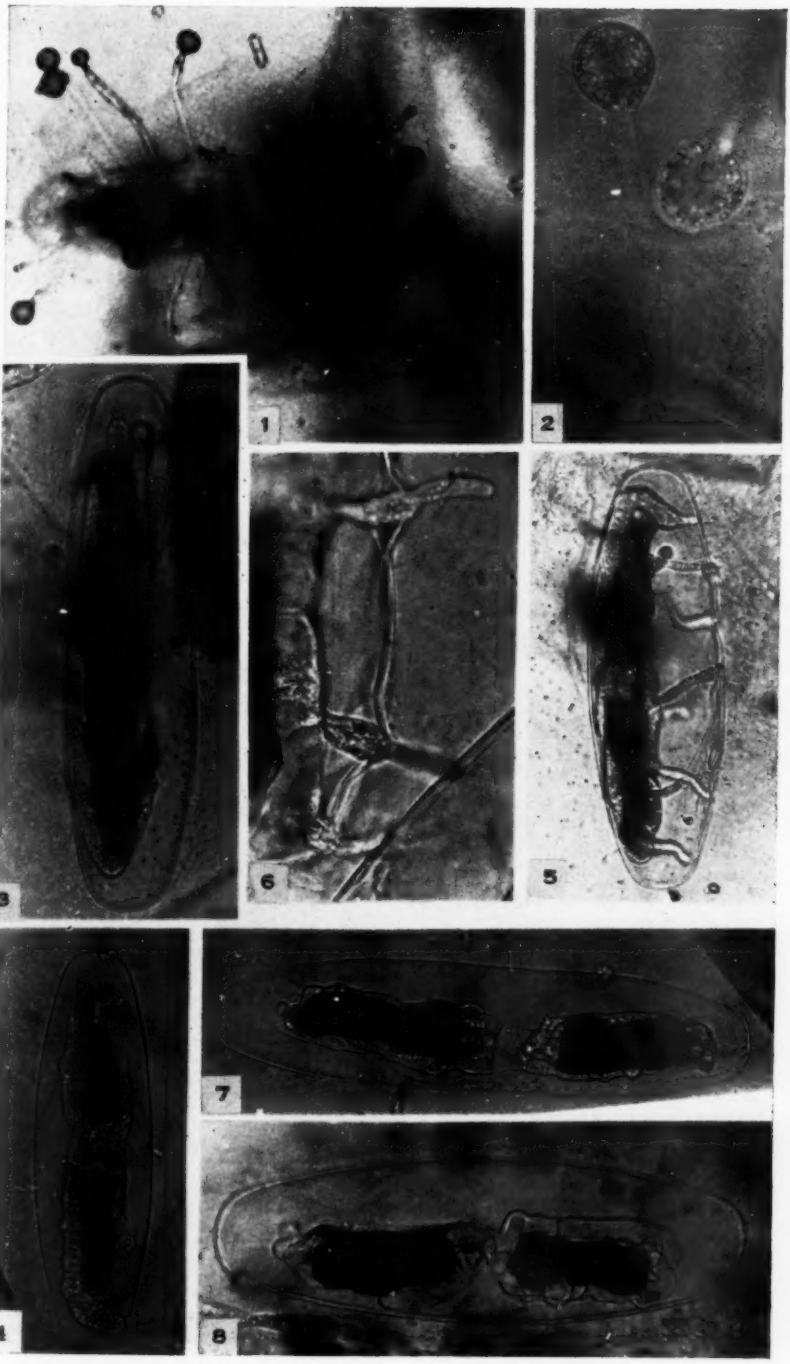
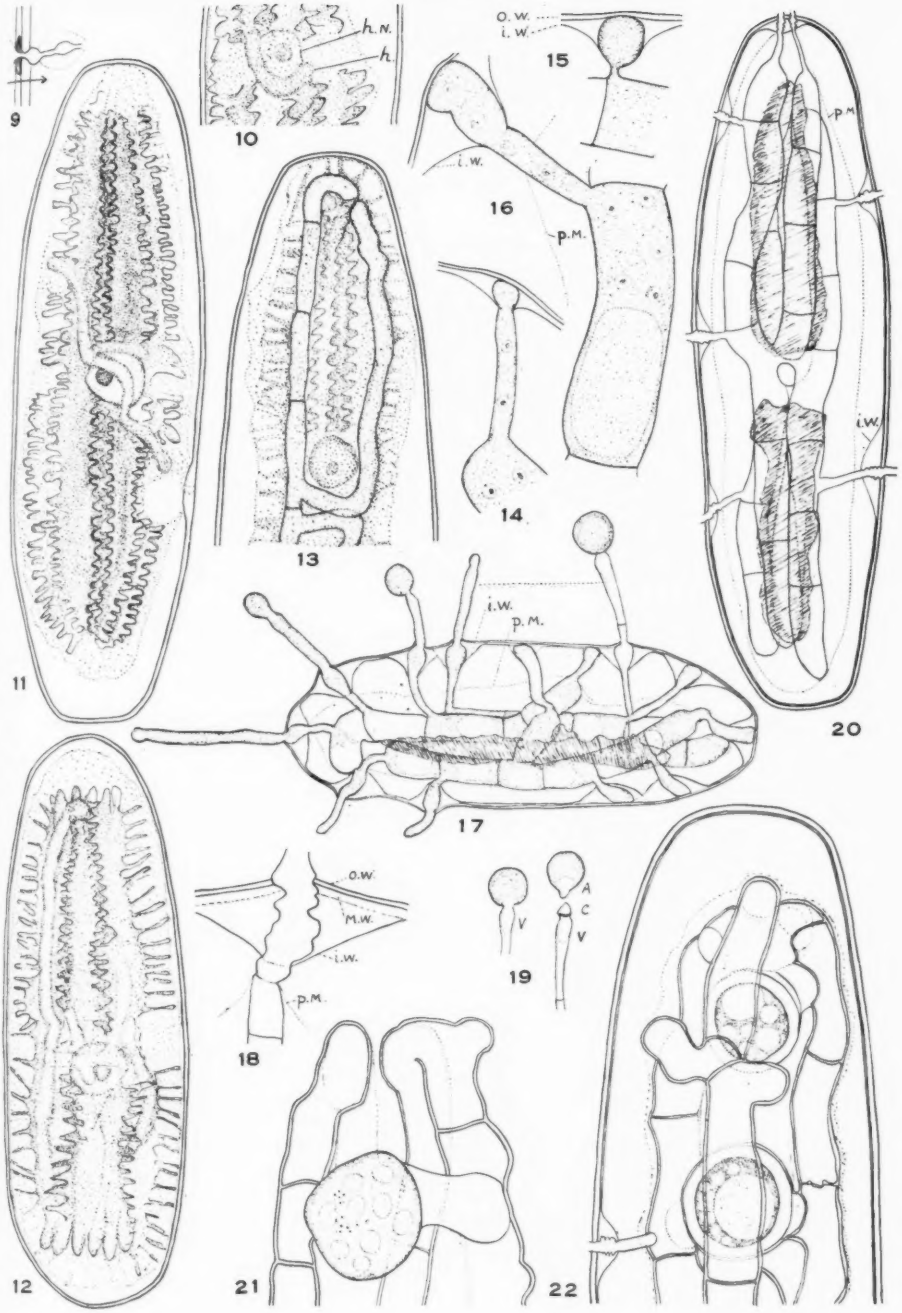


PLATE 7


9
h.N.
h.
10
O.W.
i.W.
15
i.W.
16
P.M.
14
13
P.M.
i.W.
20
11
i.W.
P.M.
17
12
O.W.
M.W.
i.W.
P.M.
18
V
A
C
V
19
21
22

A CYTOTAXONOMIC STUDY OF THE SARRACENIACEAE OF NORTH AMERICA*

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Plates 8–14

INTRODUCTION

Despite almost universal interest, both popular and scientific, in insectivorous plants the many volumes of previous work on the various genera and species do not include a thorough cytological study of the members of the Sarraceniaceae. The taxonomy, morphology, distribution, and insectivorous nature of these plants had been dealt with by Macfarlane (1908), Harper (1918), Wherry (1933) (1935), Lloyd (1942), and others; but it was only recently that Tjio (1948) working with "tropical plants" made a chromosome count as such for a plant in the genus *Sarracenia*.[1] This work with only two horticultural hybrids involved no specific or interspecific characteristics, but reported $2n=26$ for the plants investigated. The present investigation demonstrates twenty-six to be the 2n number for all species of the genus *Sarracenia*. Two previous papers, Shreve (1906) and Nichols (1908), reported twelve as the reduced number of chromosomes in three species of *Sarracenia*. These papers were not primarily concerned with chromosome number, but reported it as an observation made in the course of other studies on these plants, and may now be discounted.

GENERAL METHODS

The results and interpretations set forth in this paper were arrived at by the following several lines of investigation pursued more or less simultaneously in order that the various findings along different lines of research could be properly evaluated and compared.

A thorough review of all pertinent literature and herbarium material was made, and the type locality for each species of *Sarracenia* was visited. Collections of living plants of each species of *Sarracenia* studied were made from the type locality if possible and from other typical areas. These plants (including some of *Chrysamphora* sent from California) are growing in the greenhouse for further study and experiment. The cytological approach had not previously been applied to the two genera. Results of this approach show the two genera to be distinct and the species of *Sarracenia* to be closely related. (See section on Cy-

* This paper was condensed from a thesis presented to the faculty of the University of North Carolina in partial fulfillment of the requirements for degree of Master of Arts in the Department of Botany.

[1] Since this paper was completed for publication a chromosome count for the six Florida species of *Sarracenia* was published by Hecht in Bull. Torrey Bot. Club **76**: 7–9, 1949.

tological Methods and Results.) Because of the monotypic status of *Chrysamphora* extensive comparative field studies in this genus were not considered necessary.

GEOGRAPHICAL DISTRIBUTION

Although the specific range limits are given for each species treated in this paper, a brief summary of the general range of all plants under consideration may be of some value.

The western representative of the pitcher plants is *Chrysamphora* and is found in a limited range of northern California and extreme southwest Oregon.

Sarracenia purpurea is found more or less over the entire eastern part of North America from Canada to Florida, but the other species in the genus *Sarracenia* are found only in the southeastern part of the United States. Therefore since only the southeastern states have more than one species of *Sarracenia* they are listed here. The approximate extent and density of any specific population in relation to other members of the genus is indicated by subordinate position in the list. The number of different natural hybrids found is given for each state, but they are not listed here. See section on Natural Hybrids.

VIRGINIA, two species: *S. flava, S. purpurea.*
NORTH CAROLINA, four species, one form: *S. flava, S. purpurea, S. rubra, S. minor, S. rubra* forma *jonesii*; plus three hybrids.
SOUTH CAROLINA, four species, one form: *S. flava, S. minor, S. purpurea, S. rubra, S. rubra* forma *jonesii*; plus three hybrids.
GEORGIA, seven species, one form: *S. flava, S. minor, S. psittacina, S. Drummondii, S. rubra, S. purpurea, S. oreophila, S. rubra* forma *jonesii.*; plus three hybrids.
ALABAMA, seven species, one form: *S. Drummondii, S. Sledgei, S. purpurea, S. flava, S. psittacina, S. rubra, S. rubra* forma *jonesii, S. oreophila*; plus five hybrids.
FLORIDA, six species, one form: *S. minor, S. psittacina, S. Drummondii, S. flava, S. purpurea, S. rubra* forma *jonesii, S. rubra*; plus three hybrids.
MISSISSIPPI, five species, one form (all scarce and limited in range): *S. Sledgei, S. psittacina, S. Drummondii, S. purpurea, S. rubra* forma *jonesii, S. rubra.*
LOUISIANA, three species: *S. Sledgei, S. psittacina, S. purpurea.*
TEXAS, one species (scarce and of limited range): *S. Sledgei.*

CYTOLOGICAL METHODS AND RESULTS

All anther material used for cytological study was fixed in Craf or Carnoy's solution, stored in 70% alcohol, and smeared in aceto-orcein. No successful anther smears of *Chrysamphora* were made since all the buds of this plant sent from California were too far advanced. Root tips were also fixed in Craf or Carnoy's solution, embedded, sectioned (12μ), and stained with crystal violet.

Root tip smears were rarely successful due in part to the many cell inclusions which made observation difficult and to the small percentage of dividing cells,

even in "growing" root tips. Serial sections of root tips rarely showed much meristematic activity in any region, the roots growing very slowly (or not at all unless water were withheld from the plants for a week and then given sparingly).

All material used in the final preparation of the cytological section of this paper was taken from plants collected (except *Chrysamphora californica*, which was purchased from a collector in California) by the writer in the spring and summer of 1948. Thirty to sixty plants were collected of each species of *Sarracenia*; collections of two to ten plants were made at various stations within the general range of the species to assure the material as typical. The plants are very hardy and will stand rough treatment in transplanting if not allowed to dry out. All plants collected were planted in beds of peat in the greenhouse and marked as to collection number. Any collection number in the 2-series indicates living material, not pressed specimens. Plants were usually collected only in early bud to insure having enough material for the anther smears. Supplementary collections of buds from plants that could be positively identified in the field were often made. These buds, ranging in size from 0.6 cm. to 1.1 cm. were put in marked vials of Carnoy's solution and later stored in 70% alcohol.

A more or less definite bud size for each species was usually found which would give the desired meiotic stages. The average size of useful buds was about 0.7 cm., varying of course with the size of the plant of the species concerned; this size is reached in a week to ten days after the bud first becomes visible.

Bud collections, and thus the anther smears, were kept on an individual plant basis. The root tips, however, were collected and examined on a species basis. The mixing of root tip material from different plants within a species and from plants from different collection areas further assured "average" or "typical" cytological observations. Any irregularities would, of course, have necessitated making further collections and observations on an individual plant basis. No such collections were found necessary.

A reduced number of thirteen chromosomes was obtained for each species of *Sarracenia* (Plate 10). An unreduced number of twenty-six chromosomes, from excellent root tip material, was observed to be constant in all *Sarracenia* species (Plates 8 and 9).

The constant chromosome number throughout the genus *Sarracenia* and the lack of differentiation in regard to chromosome morphology of the various species were rather to be expected, however, in view of the ease with which the various species cross in nature or are crossed by horticulturists.

The chromosomes of all members of the genus *Sarracenia* ranged from 2.0 to 4.0 microns in length. The average chromosome length of any given genome, however, is only about 2.8 microns, since most of the chromosomes tend to be nearer the smaller extreme in length.

Slight average differences between species of *Sarracenia* will be noted, but the degree of variation is too small to be of any taxonomic value, and such average chromosomal variations as do exist between species may well be of lesser magnitude than the average variations between the genomes within a species. To emphasize the point it will be noted that the average chromosome length for *S.*

rubra is 2.75 microns while that of *S. minor* (the opposite extreme) is 2.86 microns —a difference of only 0.11 microns. Such a difference may be termed typical as far as interspecific chromosome morphology is concerned in this genus, and such differences would probably be increased or decreased by the interpretation of another worker; therefore even these small differences could not be considered constant. This average difference is exceeded somewhat in the genomes of the above mentioned two species as pictured (Plate 9, figs. 5–6). The chromosomes pictured for *S. minor* are larger than usual for this species and those pictured for *S. rubra* represent the smallest chromosomes observed within the genus *Sarracenia*. The exceedingly small size of the *S. rubra* chromosomes in this genome is accentuated by the compactness of their arrangement and by the larger, more widely spaced chromosomes of *S. minor* just below them.

The only constant character in regard to the chromosomes for any given species of *Sarracenia* is the number, the 2n number being twenty-six throughout the genus *Sarracenia*. A single chromosome with a large satellite was observed in every species of *Sarracenia* except *S. rubra*. Since this characteristic was not always observed in each species in which it was known to occur it is probable, in view of other close interspecific morphological similarities, that the genome of *S. rubra* also has such a chromosome. An unreduced number of thirty chromosomes was found in the other North American genus of pitcher plant, the monotypic *Chrysamphora*. The chromosomes of *Chrysamphora californica*, however, vary not only in number from the species of *Sarracenia*, but also in size, averaging only *ca.* 1.5 microns in length (Plate 12). Four chromosomes per genome in the California pitcher plant were slightly longer than the others. Two of these were usually observed to have a pair of large satellites each; otherwise there were no distinctive characteristics observed in this genus.

The previously mentioned numerical difference between the two genera gives further proof (if any be needed) as to their taxonomic and morphologic individuality. Further conclusions, as to the relationship of the genera, based on the two chromosome numbers would be based only on theory, and will not be attempted.

CONSIDERATIONS OF SPECIATION

It must be noted that assignment of a given individual or group of individuals to any specific or subspecific taxonomic category will depend upon the individual taxonomist's interpretation of the word "distinct" as it relates to any given difference or differences used as a basis for taxonomy.

The over-all shape or form of the pitchered leaves is generally a constant morphological characteristic, and as such is the most useful single feature used by taxonomists in species delimitation within the genus *Sarracenia*. Leaf coloration, except where constant and peculiar to a single species (as the white in *S. Drummondii* and the clear yellow-green in *S. purpurea* forma *heterophylla*), is of no taxonomic value since leaf coloration within any one species often shows most of the yellow-green-red combinations possible within this genus. The number of ensiform leaves produced is a factor of importance only in the single

extreme case of *S. oreophila*; no other related species produces these leaves in such abundance.

Flower color alone is of little value since all species normally have flowers of either one or the other of the two possible colors—red or yellow. Flower scent is a distinctive feature in two species of *Sarracenia*. *S. rubra* has a sweet scent while *S. flava* has a very singular musty odor. Petal shape varies from species to species within the genus, but it also varies considerably from plant to plant within a species. Only the extremely obovate petal shape usually found in *S. rubra* is therefore of any use to the taxonomist. This also applies to the extreme recurved condition of the sepals of *S. rubra*, the other species showing an intermediate degree of recurving, or none at all.

Size is of no value *per se* in species delimitation in this genus. Various ecological factors result in mature plants of many sizes within any given species. The extreme cases of this are shown by *S. minor* and *S. flava*, but less striking differences in size appear in all other species of *Sarracenia*. Size, therefore, is not a constant and cannot be used as a basis for taxonomic differentiation.

Some of the less obvious or microscopic morphological features found within this genus, such as pubescence or number and location of nectar glands, are not of any taxonomic value alone and may or may not be of such value when used with one or more of the grosser features of the plant.

Speciation, then, rarely depends on a single major or minor morphological characteristic, but on a group or series of characteristics considered together; and such a group must in turn be considered in relation to other such groups found within the genus.

When plants are so viewed, one is able to see not only their differences, but what is more important, their relationships. Thus in the genus *Sarracenia* leaf shape not only aids in the proper classification of the species, but shows that there are related groups of species within the genus. It will be noted as once that *S. oreophila*, *S. flava*, and *S. Sledgei* are a closely related group. *S. Drummondii*, *S. rubra*, and perhaps *S. minor* appear to be more distantly related to this same group. *S. psittacina* and *S. purpurea* may belong to another single group within the genus; but if so, they occupy rather separated positions.

From morphological comparisons and other data the most primitive or oldest member of a genus (or a larger taxonomic unit) may be determined. Since the pitcher plants are an evolved form and since there are so few members in the genus and these occupy such a comparatively limited range, a determination of the type nearest the original or parent type is difficult. *S. purpurea* is the most widespread, and therefore might be thought of as the oldest plant type in the genus. All seedlings of any *Sarracenia* have leaves the first year that are very similar to the mature leaves of *S. minor* which Macfarlane (1908) considers the most primitive. Wherry (1933) states that the yellow-green color and a range in an old geologic area indicate *S. oreophila* to be the oldest form of *Sarracenia*.

There are probably other arguments for and against each of the above theories, any one of which could be correct, but cannot be demonstrated satisfactorily at this time.

TAXONOMIC TREATMENT

The various herbaria used in the preparation of the following material are designated by the following abbreviations: NY, New York Botanical Garden; PENN, University of Pennsylvania; PH, Academy of Natural Science; US, United States National Herbarium; DUKE, Duke University Herbarium; CNC, University of North Carolina Herbarium.

KEY TO THE GENERA OF NORTH AMERICAN PITCHER PLANTS

Hood of ascidiform leaves appendaged; scape bracted, style radiate, petals bronze yellow ..... *Chrysamphora* (monotypic)
Hood of ascidiform leaves not as above, scape naked, style expanded ..... *Sarracenia*

KEY TO THE SPECIES OF SARRACENIA

Pitchered leaves erect
  Pitcher orifice more or less open
    Hood large, margins reflexed
      Hood yellow-green with slight to profuse red venation or occasionally solid red, petals yellow
        Ensiform leaves abundant, petals greenish yellow ..... 1. *S. oreophila*
        Ensiform leaves sparse or lacking
          Hood margin strongly reflexed, petals clear yellow; scent musty .... 2. *S. flava*
          Hood margin only slightly reflexed, petals cream yellow; scent none .. 3. *S. Sledgei*
      Hood white, green and red-reticulate, margins undulate, petals maroon ..... 4. *S. Drummondii*
    Hood small, margins not reflexed, petals red, often extremely obovate, sepals strongly recurved ..... 5. *S. rubra*
  Pitcher orifice covered by hood, petals yellow ..... 6. *S. minor*
Pitchers decumbent, flowers red or rarely yellow
  Orifice lateral, hood closed ..... 7. *S. psittacina*
  Orifice terminal, hood open ..... 8. *S. purpurea*

Chrysamphora californica (Torrey) Greene, Pittonia **2:** 191. 1891.
Darlingtonia californica Torr. Smiths. Contrib. **6,** art. 4: 5. 1854.

Leaves hollow, expanded upward toward inflated hood, green, more or less suffused with red-purple; hood containing many translucent blotches; orifice somewhat lateral or under protruding proximal expansion of hood, protected in a manner by two elongate, leaf-like appendages. Scape solitary, bracted, about as long as leaves. Sepals oblong, 3–5 cm. long, yellow-green on outer surface, rusty purple inside; petals 2–3 cm. long, ovate-lanceolate, narrowed toward ends, reddish-purple to bronze yellow; style short, five-lobed, radiate. Loculicidal capsule 5-valved.

Type locality: Headwaters of the Sacramento River, northern California, near Mount Shasta, growing in marshes.

Range: Bogs, from sea level at Lane County in southwest Oregon to 8000 feet in Placer Co., California.

Representative specimens: OREGON. Florence, Lane Co. *Wherry* (PH 676444); Bandon, Coos Co. *Thompson* (PH 663801); Selma, Josephine Co. *Gould 811* (NY). CALIFORNIA. Oregon Mtn., Siskiyou Co. *Wherry* (PENN); Plumas Co. *Lemmon* (PENN).

The only easily recognized feature the California pitcher plant has in common with its eastern relative is the singular form of the insectivorous leaves, and even here the appendaged hood of *Chrysamphora* differs from the simpler hood of *Sarracenia*. The flowers of the former are entirely different in form from the latter. The recognition of two genera would seem warranted without consideration of the difference in range or the difference in chromosome number.

The flowers of *Chrysamphora* (which blooms from April to July in its native habitat) are extremely long-lasting. Two plants received in bloom from California remained in bloom for well over a month when planted in the greenhouse. The leaves of *Chrysamphora*, except for the two appendages, look very much like the leaves of *S. psittacina*, but grow erect and to a much larger size. The internodes of *Chrysamphora* are somewhat larger than those of *Sarracenia*. Thus the leaves are less crowded on the rhizome and appear as a short row rather than as a cluster or basal rosette.

The western species of pitcher plant has the same basic ecological requirements as those of the southeastern species—high soil acidity and moist habitat. It grows, however, through a greater altitudinal range than any of the eastern members of this family.

No record can be found of any attempted cross between *Chrysamphora* and *Sarracenia* sp.

1. **Sarracenia oreophila** (Kearney) Wherry, Bartonia **15**: 8. 1933.
   S. flava Catesbaei Mohr, Bull. Torr. Bot. Club **24**: 23. 1897. Type loc. Ala., DeKalb Co., Lookout Mtn., bank of Little River, about 1700 feet.
   S. flava var. *oreophila* Kearney, nomen nudum, Science **12**: 837. 1900. Type loc. Lookout Mtn., especially near its southwest end in Alabama.
   S. Catesbaei Elliott, of Mohr (*not* Elliott), Plant Life of Alabama, p. 531. 1901.
   S. flava in part, certain authors (as to localities).

Summer leaves green, erect, ascidiform 3–7 dm. tall, well developed at flowering time, hood suberect, rounded, apiculate, moderately constricted at base, slightly if at all revolute; winter leaves flat, ensiform, recurved, numerous, 1–2 dm. long in basal rosette. Scape about as high as summer leaves. Sepals green, 3–5 cm. long, widest near middle, rounded at apex; petals greenish-yellow, narrowly fiddle-shaped, 4–5.5 cm. long, widest at expanded basal portion; style disk 3–6 cm. in diameter, pubescent. Mature capsule 0.75–2 cm. in diameter.

Type locality: Alabama. DeKalb Co., Lookout Mtn., bank of Little River near DeSoto Falls.

Range: Rare along sandy stream banks in the mountains of northeastern Alabama and extreme west central Georgia. Also reported by Wherry from Elmore Co., Alabama.

Representative specimens: ALABAMA. Flat Rock, Jackson Co. *Wherry* (PENN); Valley Head, De Kalb Co. (US 980565); Little River, Mentone, Cherokee Co. *Bell 510* (CNC); Center, Cherokee Co. *Harper* (US).

S. oreophila in its small, more or less mountainous, inland range blooms about

the middle of May. The plants in Elmore County, Alabama, probably bloom somewhat earlier; but no plants were observed or collected in that area despite extensive searching during March, 1948.

The flowers of *S. oreophila* are similar to those of *S. flava*, to which it is obviously closely related, but the petals are narrower; and although Wherry says in his description of the species that the flowers have a faint musty scent, those collected along the east bank of the Little River below Mentone, Alabama, for this study had no noticeable odor, musty or otherwise.

Several workers prior to Wherry had recognized the plants of *Sarracenia* collected in northeastern Alabama as being different from "typical" *S. flava* and had made various attempts at naming them. Mohr (1897) first named these plants *S. flava Catesbaei* in his "Notes on some undescribed and little known plants of the Alabama Flora," believing them to be identical with *S. Catesbaei* Elliott (1824). Four years later in his "Plant Life of Alabama" Mohr raised these plants to specific rank, as *S. Catesbaei* Elliott. Elliott's *S. Catesbaei* described in 1824 from specimens collected "along the margins of rivulets amidst the high sand hills of Chesterfield district in S. C." by Macbride were considered by Croom, who saw Elliott's specimen, to be *S. flava* and by Macfarlane who annotated the specimen to be a natural hybrid between *S. flava* and *S. purpurea*. Macfarlane's evaluation of *S. Catesbaei* Elliott is doubtless correct and such hybrids bear that name at the present time. The inapplicability of the name *Catesbaei* to the plants of N.E. Alabama collected by Mohr is obvious. Meantime Kearney (1900) apparently unaware of Mohr's plants named plants observed at the locality of Mohr's previous collections *S. flava* var. *oreophila*, but did not describe them. Macfarlane (1908) does not recognize the plant, but cites a collection of *S. flava* from Valley Head, Ala., and notes Mohr's name of *S. Catesbaei* in connection with it. Harper (1918) recognized Kearney's name, *S. flava* var. *oreophila*; finally, Wherry (1933), recognizing the distinctiveness of the plant, has supplied a complete description of the plant and named it *S. oreophila*.

The name *Catesbaei* has thus been removed from specific rank in the genus *Sarracenia*. This is indeed fortunate, for many of the early botanists seem to have applied the name, along with very sketchy if not inaccurate descriptions, to several different new, odd, or otherwise unidentified plants of *Sarracenia*, and any present use of the name in a specific capacity would only add to the taxonomic confusion surrounding it.

Aside from the lack of scent, which is so strong in *S. flava*, *S. oreophila* also differs from that species in having many more flat winter leaves, many of which are strongly recurved. The ranges of the two species are very distinct and the habitats differ. *S. oreophila*, instead of being found in bogs, usually occurs in sandy pockets along stream banks, often in the shadow of *Kalmia* and *Rhododendron* rather than in association with *Drosera* or *Pinguicula*. The extremely restricted range of *S. oreophila* may be enlarged slightly by further study, but at present it is the only species completely disjunct from all other members of the genus *Sarracenia*. There are several unconfirmed reports of this species

from northwestern Georgia. Although there is no herbarium specimen of any *Sarracenia* from Tennessee, Gattinger reported its presence there and A. M. Jennison reports finding a plant of the genus *Sarracenia* in Fentress County, Tennessee, which may be *S. oreophila*, according to A. J. Sharp, who was with the group that found the plant and who later compared it mentally with *S. oreophila* in the greenhouse at the University of North Carolina.

2. **Sarracenia flava** L. Sp. Pl. **1:** 510. 1753.

S. Gronovii var. *flava* Wood, Class Book, p. 222. 1861. Type loc. Va. to Fla. and La.

S. Rugelii, Shuttlew. Msc. ex A. DC. Prod. **17:** 6. 1873.

S. flava var. *atropurpurea* Hort. Bull, in Gard. Chron. 759. 1880.

S. flava var. *atro-sanguinea* Hort. Bull ex André, Illustr. Hortic. **17:** pl. 386. 1880. Cat. Hort. Bull et Masters, Gard. Chron. ser. 2, **16:** 12. 1881.

S. flava var. *limbata* Cat. Hort. Bull et Masters, Gard. Chron. ser. 2, **16:** 12. 1881.

S. flava var. *maxima* Masters, Gard. Chron. ser. 2, **16:** 12. 1881.

S. flava var. *minima* Masters, Gard. Chron. ser. 2, **16:** 12. 1881.

S. flava var. *ornata* Cat. Hort. Bull et Masters, Gard. Chron. ser. 2, **16:** 12. 1881.

S. Fildesii Hort. Nicholson, Dict. of Gard. **3:** 363. 1886.

S. flava var. *Rugelii* Shuttlew. msc. ex Masters, Gard. Chron. **16:** 11. 1881.

S. flava var. *media* Macfarlane in Engl. Das Pflanzenreich **4,** pt. 110: 31. 1908.

Summer leaves erect, elongate, trumpet-shaped with narrow linear wing, 4–12 dm. tall, expanding gradually from base to orifice; hood suberect, rounded, apiculate, narrow at base, edges revolute; color yellow, green or red, the first two often more or less reticulate with reddish-purple veins. Winter leaves ensiform, 2–4 dm. long. Scape usually slightly shorter than the summer leaves. Flowers with a strong musty scent; sepals green, 3–5 cm. long, widest near middle, rounded at broad apex; petals yellow, 5.5–10 cm. long (usually 5.5–7 cm.), narrowly obovate, slightly widened near base; style-disk 3–9 cm. broad (usually 4–8 cm.), the lobes 2-cleft at apex. Mature capsule 1–2.5 cm. in diameter.

Type locality: "Hab. in Americae septentrionalis udis."

Range: Bogs, swamps, low, open pine woods. Southeastern Virginia through eastern North Carolina and South Carolina to southeastern Georgia, thence west through southern Georgia and northern Florida to the vicinity of Mobile, Alabama.

Representaive specimens: VIRGINIA. New Bohemia, Prince George Co. *Wherry* (PENN); Cadayshore, Sussex Co. *Fernald* and *Long 6212* (PENN). NORTH CAROLINA. Kilkenny, Tyrrell Co. *Godfrey* and *Kerr* (DUKE 55389); Burgaw, Pender Co. *Bell* (CNC); Method, Wake Co. *Godfrey 3775* (CNC); Harmony, Iredell Co. *Radford 2633* (CNC); Lenoir, Caldwell Co.

Wherry (PH 753322). SOUTH CAROLINA. Hartsville, Darlington Co. *Smith* (CNC 26579); Georgetown, Georgetown Co. *Coker* (CNC 3104); Walterboro, Colleton Co. *Wherry* (PENN). GEORGIA. Graymont-Summit, Emanuel Co. *Wherry* (PENN); Alma, Bacon Co. *Harper 468* (PH); Quitman, Brooks Co. *Pyron* and *McVaugh* (DUKE 09238); Coolidge, Thomas Co. *Coker* and *Harbison* (CNC 31321). FLORIDA. Blountstown, Calhoun Co. *Bell* (CNC); Ponce de Leon, Holmes Co. *Lambert* (PENN); Crestview, Okaloosa Co. *Blanton* (US 1485419). ALABAMA. Kinston, Coffee Co. *Wherry* (PENN); Geneva, Geneva Co. *Wherry* (PENN).

S. flava is usually the first of the Sarracenias to bloom in any given locality within its range. The blooming season starts about March 15 at the southern limit of the range and ends near the last of May at the northern limits of the range and at the slightly higher elevations in the piedmont section of North Carolina.

The flowers of this species are bright yellow and have a strong musty scent not found in any of the other Sarracenias. Rarely the flower is erect instead of drooping, the petals in this case radiating to give the flower a somewhat star-shaped appearance.

This species does not have as great a range as *S. purpurea*, but is probably the most common of the genus, and shows more variety in leaf size and coloration than any other species of *Sarracenia*.

Some of these variations from the average are worthy of citation. Specimens of extreme size are: Fayetteville, Cumberland Co., North Carolina, *Wherry* (PENN), the leaves approaching 10 dm. in length; Wilmington, Brunswick Co., North Carolina, *Macfarlane* (PENN 49557), one leaf being 7.5 dm. tall and having a hood 13.5 cm. across; Ponce de Leon, Holmes Co., Florida, *Macfarlane* (PENN 38533), pitchered leaf only 6.5 dm. tall, but extremely broad at the upper portion, the hood being 14.7 cm. across. Specimens showing relatively extreme coloration are: Dalkeith, Gulf Co., Florida, *Moldenke 1148* (NY), leaf yellow, very little red at throat only; Santee, Charleston Co., South Carolina, *Bell 515* (CNC), leaf almost solid maroon.

Many of these variations have been given varietal rank by previous workers, but field observations and a study of herbarium material show that most of them are not definite or constant enough to be recognized as such and therefore are not given taxonomic importance here. Some such plants are: *S. Rugelii* Shuttlew. *Rugel*, Quincy, Gadsden Co., Florida (NY); *S. flava* var. *minima* Masters *Tracy*, St. Andrews Bay, Bay Co., Florida (PENN 49550); *S. flava* var. *ornata* Masters *Tracy*, St. Andrews Bay, Bay Co., Florida (PENN 49549).

It will suffice to say that the ascidiform leaves do vary not only from habitat to habitat but from clone to clone within a small habitat area. The most striking example of this was seen in a bog near Santee, South Carolina, where plants with clear yellow leaves, plants with solid red leaves and plants with leaves mottled to various degrees with red or maroon grew side by side.

Some extreme plants of *S. flava* have leaves of a solid dark red color. This very striking plant does not appear in isolated patches in a particular type of

habitat, but appears among extensive stands of typical yellow, green, or variegated-leaved *S. flava*. Although the proportion of plants with this extreme coloration is rather small in a given number of plants of *S. flava*, several hundred of them have been observed in an extensive stand of *Sarracenia* near Georgetown, South Carolina, and also in a stand near Santee, South Carolina. No plant of this variant of *S. flava* has ever been observed with flower or fruit or any evidence of either, although a pointed search was made for such evidence. This form does not appear to be basically an ecological form, but rather a genetic form with many intergrades between it and its solid green or yellow-leaved relatives. Macfarlane (1918) noticed that the red-leaved plants lost much of their red coloration when planted in the greenhouse. Such observations were also made by the present writer on plants brought in for this study. The extreme red coloration observed in some plants of *S. flava* in the field then seems to be a genetic capability rather than a genetic constant. Plants of this species that grow in somewhat shaded areas tend to have solid green leaves with only a reddish-purple band across the inner surface of the narrow neck of the hood and a minimum of red-purple reticulation around the orifice.

The range of *S. flava* overlaps or includes the ranges of all other species except *S. oreophila* and *S. Sledgei*. Of the six species thus within its range *S. flava* hybridizes with four (possibly more, but as yet unreported). See treatment of reported natural hybrids, *S. purpurea* x *flava*, *S. Drummondii* x *flava*, *S. minor* x *flava*, and *S. rubra* x *flava*.

3. **Sarracenia Sledgei** Macfarlane, Jour. Bot. **45:** 4. 1907; Engl. Das Pflanzenreich **4,** pt. 110: 29. 1908.

S. Gronovii var. *alata* Wood, Class Book, p. 222. 1861. Type loc. Louisiana, *Hale*.

S. flava var. *crispata* Masters, in Gard. Chron. ser. 2, **16:** 12. 1881.

Summer leaves erect, elongate, trumpet-shaped with narrow linear wing, 2–8 dm. (usually 3–6 dm.) tall; hood suberect, ovate, apiculate with relatively straight inconspicuous red veins, edges flat or only slightly revolute. Scape about as long as the leaves. Sepals yellow-green, 2.5–5 cm. long, widest near base, tapering to narrow, blunt apex; petals light cream-yellow or greenish-yellow, fine-textured, 4–6 cm. long, obovate, often more or less revolute, distinctly expanded, measuring about 1.5 cm. across at its widest point; style disk 2.5–6 cm. in diameter, the lobes 2-cleft at apex. Capsule 1–2 cm. in diameter.

Type locality: West of Mobile River near Theodore, Ala., *Macfarlane*.

Range: More or less common in the southwestern quarter of Alabama west of the Mobile River and westward through southern Mississippi and Louisiana into the more humid areas of eastern Texas.

Representative specimens: ALABAMA. Deer Park, Washington Co. *Reade* (PENN 57861); Mobile, Mobile Co. *Macfarlane* (PENN 1542); Theodore, Mobile Co. *Bell 547* (CNC). MISSISSIPPI. Orange Grove, Jackson Co. *Bell 546* (CNC); Mississippi City, Harrison Co. *Canby* (US 369633). LOUISIANA. Abita Springs, St. Tammany Co. *Pennell* (PENN 58980). TEXAS.

Rust Co. (US 1468840); Tyler Co. *Whitehouse 756* (NY); Newbaden, Robertson Co. *Barkley 13006* (NY).

S. Sledgei, like *S. flava*, is the first of the pitcher plants to bloom within its range, being in full bloom near Mobile, Alabama, shortly after March 15 and continuing to bloom until the middle of April or possibly later further inland from the Gulf coast. The flowers of this species have a finer-textured petal than any of the other Sarracenias. Also this is the only species often having revolute petals, the majority of the plants observed in bloom just west of Theodore, Alabama, having petals more or less broadly revolute (Plate 13, figs. 2 and 3).

Before *S. Sledgei* was recognized and described as a new species by Macfarlane in 1908, it was considered to be *S. flava* or at best a western form of *S. flava*. However, the leaves are smaller and narrower than those of *S. flava* and seldom show the varied coloration or the revolute hood of that species. No plants of *S. Sledgei* seen in the field approached the dark red extreme possible in this species as evidenced by two of Macfarlane's collections: Ocean Springs, Jackson Co., Mississippi, *Macfarlane* (PENN 38501); Slidell, St. Tammany Co., Mississippi, *Macfarlane* (PENN 39673). In the first specimen the upper portion of the leaf and the hood are almost solid red; in the second specimen cited the leaf is colored to a lesser degree, but still has far more red pigmentation than average for *S. Sledgei*.

Although *S. Sledgei* is the only member of the genus *Sarracenia* found west of the Mississippi River, the eastern part of its range coincides with parts of the ranges of *S. Drummondii*, *S. purpurea*, *S. psittacina* and *S. rubra*; and in one small wet pasture south of highway U. S. 90 just west of Theodore, Alabama, *S. Sledgei* was found growing with the last three mentioned. It was at this location that what seems to be a previously unreported natural hybrid was collected, *Bell 2-29*. See treatment of natural hybrids *S. Drummondii* x *Sledgei* and *S. purpurea* x *Sledgei*.

4. **Sarracenia Drummondii** Croom, Ann. Lyc. Nat. Hist. **4:** 100. 1848.
?*S. lacunosa* W. Bartram, Travels, p. 417. 1791.
S. leucophylla Raf. Fl. Ludov., p. 14. 1817.
S. undulata Decne. Rev. Hort. **1:** 126. 1852.
S. Gronovii var. *Drummondii* Wood, Class Book, p. 222. 1861.
S. laciniata Kerner, Pflanzenleben, ed. 1, **1:** 118. 1887.

Summer leaves erect, elongate, trumpet-shaped with narrow linear wing, 4–12 dm. tall, the gradually expanding upper portion white, reticulate with red-purple veins; hood colored as upper portion of leaf, sub-erect, ovate or orbicular, margins undulate, contracted at base, inner surface more or less hispid. Winter or late summer leaves more or less numerous, ensiform or with extremely reduced pitchers and large linear wings, 2–6 dm. tall, in basal rosette. Scape erect, about as tall as the summer leaves. Sepals dark red, ovate, narrow apex slightly rounded, 2–4 cm. long; petals dark red, fiddle-shaped, usually widest at expanded basal portion, 4.5–7 cm. long; style disk 4–6 cm. in diameter, lobes 2-cleft. Capsule 1–2.5 cm. in diameter.

Type locality: Near the town of Appalachicola in Florida, *Drummond* in 1835.

Range: Southwestern Georgia and northern Florida near Tallahassee westward through northern Florida and southern Alabama into southeastern Mississippi. Common only in the southern half of the range, especially around Mobile, Alabama.

Representative specimens: GEORGIA. Americus, Sumter Co. *Wherry* (PENN). FLORIDA. Dead Lakes, Liberty Co. *Small* (US 1739079); Appalachicola, Gulf Co. *Moldenke 1177* (PENN); Fountain, Bay Co. *Bell 540* (CNC); Crestview, Okaloosa Co. *Macfarlane* (PENN 49350). ALABAMA. Flomaton, Escambia Co. *Macfarlane* (PENN 38510); Gateswood, Baldwin Co. *Tracy* (PENN 50666); Whistler, Mobile Co. *Graves* (US 1085034). MISSISSIPPI. Gulfport, Harrison Co. LeClair (CNC 3102).

S. Drummondii starts to bloom about the last week in March or slightly later than the other species of *Sarracenia* within its range. The main blooming period for the species as a whole is short, since it has a relatively small range restricted in depth from the Gulf coast and thus of a more or less uniform climate. The flowers of *S. Drummondii* are nodding at anthesis as are those of all the other members of the genus, but they commonly become more and more erect until they are perfectly erect by the time the petals drop. This habit was not observed (except in rare cases in *S. flava*) in any other species.

Color gradients are found in the foliage of *S. Drummondii* as in most other species of the genus, but do not seem to approach the dark red extremes often found in *S. purpurea* and *S. flava* except in rare cases. None of the dark red plants of *S. Drummondii* were observed in the field, but a plant of this color from Crestview, Florida, in Macfarlane's collection at the University of Pennsylvania and labeled *S. Drummondii* var. *atropurpurea* (*Macfarlane*, PENN 49355) seems to be a typical specimen of one extreme of color expression possible within the species. Another specimen from Deer Park, Alabama (*Reade*, PENN 57858) was labeled *S. Drummondii* var. *rubra*, but appeared to be of typical color with no excessive red pigmentation in the leaves. A plant approaching the lighter extreme of coloration had very pale green leaves with no red except along the veins in the hood and around the pitcher orifice. This plant was also collected at Deer Park, Washington Co., Alabama, and was labeled *S. Drummondii* var. *alba* (*Reade*, PENN 57857). All of the above plants are here considered as *S. Drummondii*. The differences in degree of red coloration are to be expected and should be noted, but not given taxonomic importance.

The white-topped leaves of *S. Drummondii* are very distinctive and offer a most striking color contrast to the usual bog vegetation. Harper (1918) says that the showy leaves have often been mistaken for the flowers by many nonbotanists. *S. Drummondii* grows in shady bogs or on moist sandy slopes. Its range, though small, coincides with parts of the ranges of every other species of *Sarracenia* except that of *S. oreophila*; and three different natural hybrids of *S. Drummondii* have been reported. See treatment of reported natural hybrids, *S. Drummondii* x *flava*, *S. Drummondii* x *purpurea* and *S. Drummondii* x *Sledgei*.

5. **Sarracenia rubra** Walt. Fl. Carol., p. 152. 1788.

S. Gronovii var. *rubra* Wood, Class Book, p. 222. 1861.

Type loc. Va. to Fla. and La.

S. minor Sweet, Brit. Flower Gard. ser. 2., t. 138. 1831–38.

S. Sweetii DC. Prodr. **17**: 5. 1873.

S. rubra var. *acuminata* DC. Prodr. **17**: 4. 1873.

Leaves numerous, dull green, usually finely but profusely reticulated with maroon-purple around the orifice and inner surface of the hood, 1–5 dm. long, narrow pitcher expanding gradually from base to orifice; hood suberect, ovate, acuminate, usually more or less closely covering orifice, not contracted at base; wing narrow, usually linear, sometimes slightly wider at or below the middle. Scape erect, usually taller than leaves. Flowers sweet-scented; sepals maroon on outside with green inner surface, ovate, 2–3 cm. long, obtuse, very strongly recurved soon after the petals fall; petals maroon, often yellow-green tinged with red on inner surface, 2.5–4 cm. long, obovate, often extremely so; style disk 2–3.5 cm. in diameter, 2-cleft at apex. Mature capsule 0.5–1.5 cm. in diameter.

Type locality: South Carolina.

Range: Not common, usually in relatively small, inconspicuous patches in bogs, swamps, and open pine or mixed forests from southeastern corner of North Carolina southwest in a broad band across South Carolina into central Georgia and on into western Florida, southern Alabama and southeastern Mississippi. The disjunct range centering around De Funiak Springs, Florida, shown by Wherry in his series of distributional maps for the species of *Sarracenia* seems to have been delimited too closely, a group of plants of *S. rubra* having been collected in connection with this work west of Theodore, Alabama (*Bell 2-27*). Studies of herbarium material have tended further to break down the argument for disjunct ranges for *S. rubra* and *S. jonesii* as listed by Wherry (Plate 12).

Representative specimens: NORTH CAROLINA. Vass, Moore Co. *Bell 521* (CNC); Wilmington, Brunswick Co. *Wherry* (US 1466408). SOUTH CAROLINA. Hartsville, Darlington Co. *Smith 276* (CNC); Georgetown, Georgetown Co. *Godfrey* and *Tryon 210* (PENN); St. Mathews, Calhoun Co. *Schallert* (DUKE 01801). GEORGIA. Erick, Montgomery Co. *Harper* (NY); Ohopee, Tattnall Co. *Harper* (US 511165); Toadover Creek, Macon Co. *Reynolds* (PH 745311). FLORIDA. Deerland, Okaloosa Co. *Bell 526* (CNC); Crestview, Okaloosa Co. *Leeds* (PH 724843). ALABAMA. Bay Minette, Baldwin Co. *Macfarlane* (PENN 39682); Theodore, Mobile Co. *Bell 576* (CNC). MISSISSIPPI. Waynesboro, Wayne Co. *Pollard* (NY).

S. rubra is a rather late-blooming species, not being in full bloom until the last half of April at the southern limits of its range and not blooming until mid-May in North Carolina. The flowers have a sweet scent similar to that of violets, and are small and rather delicate when compared to the sturdy, odorless flowers of *S. purpurea*. The sepals of *S. rubra* are more strongly recurved, and begin to recurve at an earlier date after anthesis than in any other species of *Sarracenia* (Plate 11, fig. 3). *S. purpurea* is at the other extreme, rarely showing any tendency of the sepals to recurve (Plate 11, fig. 2). The petals of *S. rubra* also differ from those of all other plants of the genus by being extremely obovate,

the distal lobe often being twice the width of the basal lobe and as much as five times the width of the narrow neck between the two lobes (Plate 11, fig. 1). A double-flowered plant of this species was reported from South Carolina by W. C. Coker (Plant World **12**: 253. 1909). The leaves of *S. rubra* are dull green with the only coloration being the maroon lip of the orifice and the light reticulation of the hood; thus they are not at all showy, and their small size makes the isolated clumps hard to spot in the field.

Like all the pitcher plants, *S. rubra* is a hydrophyte, but it has been collected in several localities that seemed slightly drier than usual. The linear southwest-northeast range of *S. rubra* coincides with parts of the ranges of all other plants of the genus except *S. oreophila*. Yet only two natural hybrids have been reported; see *S. purpurea* x *rubra* and *S. rubra* x *flava*.

5a. **Sarracenia rubra** forma **jonesii** (Wherry) n. comb.

S. jonesii Wherry, Journ. Wash. Acad. Sci. **19**: 385. 1929. Type loc. south of Flat Rock Station, Henderson Co., N. C., *Wherry* in 1922 (US 1438266).

Differs from species type in usually having longer leaves that are more distinctly expanded toward the orifice (Plate 11, figs. 4 and 5). The hood may also be somewhat higher over the orifice than in *S. rubra*.

Type locality: Moist meadow 1.5 miles south of Flat Rock Station, Henderson County, North Carolina.

Range: Scarce in wet meadows and along stream banks in an isolated northern section of its range, including Buncombe and Henderson counties in North Carolina and Pickens Co. in South Carolina. Occasional throughout the range of *S. rubra*, but more common in its coastal range of southern Alabama, the western portion of northern Florida and extreme southeastern Mississippi.

Representative specimens: NORTH CAROLINA. Flat Rock, Henderson Co. *Wherry* (US 1438266); Biltmore, Buncombe Co. Biltmore Herbarium 3374a (NY). SOUTH CAROLINA. Mtn. Lake, Pickens Co. *Bell 573* (CNC); Kershaw, Lancaster Co. *House* (US 514174); Strother's Pond, Batesbury, Saluda Co. *McGregor* (US 1074983); Sumter Co. *Holdaway 29* (DUKE 42645). GEORGIA. Ohopee, Tattnall Co. (NY). FLORIDA. Margins of swamps, Walton Co. *Curtiss* (US 3031). ALABAMA. Jasmine, Chilton Co. *Harper* (US 1085323); Deer Park, Washington Co. *Reade* (PENN 57854). MISSISSIPPI. Poplarville, Pearl River Co. *Langman 1937* (PENN); Saucier, Harrison Co. *Oosting 1892* (DUKE).

S. rubra forma *jonesii* blooms the latter half of April with *S. rubra* in its southern range, and the last two weeks of May in its northern mountainous range. The flowers of the form are exactly like those of the species, having the sweet scent, extremely obovate maroon petals, and the strongly recurved sepals of typical *S. rubra*. The leaves of the form, as mentioned above, differ somewhat from those of the species; but leaf shapes intermediate between the two are so common in southern Alabama and northwestern Florida that it is difficult to classify any but those near the extremes (Plate 11, fig. 6).

The main difference between *S. rubra* and Wherry's species *S. jonesii* seemed

to be one of size, many large specimens with typical *S. rubra* leaf form being labeled *S. jonesii* (by Wherry) in the various herbaria. Since leaf size is seen to vary greatly in several other species, notably *S. minor* and *S. flava*, it should not be given too much importance in species delimitation. The only factor considered here in separating *S. rubra* from forma *jonesii* is leaf shape. Any plant within this species having leaves that are in general sharply expanded toward the rather exposed orifice (Plate 11, figs. 5, 6a & b) are placed in the *S. rubra* forma *jonesii* classification, and any plants with leaves in general conforming to a more uniform taper toward the more or less closely covered orifice (Plate 11, figs, 4, 6c & j and Plate 13, fig. 4) are considered typical of *S. rubra*. Often the leaves of forma *jonesii* are taller than those of the species, but this is not always true (Plate 11, fig. 6d). In so far as most intergrades tend toward the species characteristic they are classified with this taxonomic unit rather than with the form (Plate 11, fig. 6e, f & g).

No plants of Wherry's *S. jonesii* could be found at the type locality. Living plants sent to me by Mr. Rodgers from a location in Pickens County, previously reported by the late Dr. Ives, had leaves so similar to typical *S. rubra* that positive identification could not be made at that time. Later the plants produced a few of the larger leaves upon which the form is based (Plate 13, fig. 8). Plants subsequently observed in Pickens County, South Carolina, also had both types of leaves. And some plants of typical *S. rubra* from Moore County, North Carolina, grown in the greenhouse have shown a tendency to produce leaves with more sharply expanded upper portion and hoods more erect than usual (Plate 13, fig. 5).

From the relatively small amount of living and herbarium material available for the study of *S. rubra* forma *jonesii* as it occurs in the mountains of North and South Carolina it appears that it is the dominant, if not only, expression of the species in this area (Plate 13, fig. 8). However, since its floral characteristics are identical with those peculiar only to *S. rubra*, and since the ranges of the two types coincide at other locations, the large-leaved plants are not here considered of specific importance.

6. **Sarracenia minor** Walt. Fl. Carol., p. 153. 1788.
S. lacunosa Bartr. Travels, p. 417. 1791.
S. variolaris Michx. Fl. Bor. Am. **1:** 310. 1803.
S. adunca Smith, Exot. Bot. **1:** 103. 1804.

Leaves erect, usually 2–6 dm. long, gradually expanding upward from the base; outer edge of wing almost straight from base of leaf to orifice, being extremely narrow at these two extremes and widest in the middle, the curve of the wing thus complementing the curve of the tubular portion of the leaf; hood ovate, arching, incurved over orifice, hood and upper portion of leaf heavily maculated with white or opaque blotches and variegated with green and red-purple veins. Scape erect, usually shorter than the leaves. Sepals ovate, 1–3 cm. long, obtuse; petals narrowly fiddle-shaped, clear yellow, the slightly expanded basal portion often being more or less red, especially on the inner surface; style disk 2–3 cm. in diameter, 2-cleft at the apex. Mature capsule 0.75–1.5 cm. in diameter.

Type locality: "From South Carolina to Florida."

Range: Common in bogs, swamps, low fields, and open pine woods from the southeastern corner of North Carolina near Wilmington through the southeastern half of South Carolina and Georgia almost to Alabama, thence through northeast Florida and southward in central and east coastal peninsular Florida to the Everglades (?).

Representative specimens: NORTH CAROLINA. Fayetteville, Cumberland Co. *Clark* (DUKE 92956); Columbus Co. *McCarthy* (US 3034); Southern Pines, Moore Co. *Harriot* (PH 815525). SOUTH CAROLINA. Hartsville, Darlington Co. *Smith* (CNC 26578); Sumter Co. *Harper* (NY); Manning, Clarendon Co. *Godfrey* and *Tryon* (US 1837684); Georgetown, Georgetown Co. *Bell 577* (CNC); Summerville, Dorchester Co. *Hollinhead* (PENN 1568). GEORGIA. Statesboro, Bulloch Co. (DUKE 33967); Lyons, Toombs Co. *Oosting* (DUKE 49600); Waycross, Ware Co. *Bell 527* (CNC); Okefenokee, Ware Co. *Harper 1476* (NY) also *Bell 529* (CNC); Leesburg, Lee Co. *Wherry* (PENN). FLORIDA. Penney Farms, Clay Co. *Totten* (CNC 28973); Oviedo, Seminole Co. *Walker 1756* (PENN); Kissimee, Osceola Co. *Williams* (PH 636964); Sebring, Highlands Co. *Correll* and *McFarlin* (DUKE 46244); Tallahassee, Leon Co. *Ashe* (CNC 31311).

S. minor is intermediate in blooming date north of peninsular Florida, where its range coincides with other plants of this genus, blooming the last two weeks in April at the southern limit of its mainland range and slightly later further north and/or inland. The flowers of *S. minor* are odorless, clear yellow (Walter's first but unpublished name for this species was *S. lutea.*), and vary greatly in over-all size, depending upon the size of the plant. The petals, for instance, averaging 2.5-4 cm. in length for the smaller or average size plant and averaging 4.5-6 cm. in length for the large plants found in the Okefenokee Swamp in southeastern Georgia. The large plants collected by boat in the Okefenokee are similar to the typical *S. minor* of drier habitats in every respect except size. Some of the plants collected had leaves ten or more decimeters long and were growing on (or in) floating "islands" of rotting vegetation in the swamp. The first new set of leaves put out by these same plants growing under somewhat drier conditions in the greenhouse averaged less than 7.5 dm. However, the smaller *S. minor* plants collected in an open pine field only a few miles outside the Okefenokee did not show any appreciable increase in the leaf size when grown in the greenhouse although they probably received as much or possibly more water than in their native habitat. The extremely large plants of *S. minor* found in the Okefenokee Swamp and mentioned by several previous writers thus seem to be only an ecological form, dependent upon habitat for their singular variation.

Yet not all plants from the Okefenokee have extremely large leaves. One plant collected in bloom in this area, *Reade* (PENN), had leaves only 14 cm. long. Quite a few plants of *S. minor* on file from areas other than the Okefenokee Swamp approached the size of the average plants of this area, one from Myrtle Beach, Horry Co., South Carolina (*Doubles et al.*, CNC 10820) having a leaf 42 cm. long.

A plant collected by R. M. Harper in Coffee Co., Georgia, was originally labeled *S. lacunosa* (*Harper*, US 384553), but had been annotated "minor" by some later observer. It looked like typical *S. minor*.

S. minor does not grow very far westward, its range bulging inland from the Atlantic coast to a point near Tallahassee, Florida. This lack of longitude is more than compensated for in its range of latitude, however, since the plant is found from North Carolina to Florida and is the only one of the genus really to penetrate peninsular Florida. Its range is coincident with parts of the ranges of *S. flava*, *S. psittacina*, *S. purpurea*, *S. rubra* and *S. Drummondii*, hybrids between *S. minor* and the first two having been reported. See *S. minor* x *flava* and *S. minor* x *psittacina*.

7. **Sarracenia psittacina** Michx. Fl. Bor. Amer. **1:** 311. 1803.
S. calceolata Nuttall, Trans. Amer. Phil. Soc. ser. 2, **4:** 49. 1834.
S. pulchella Croom, Amer. Jour. Arts. Sci. **25:** 75. 1834.

Leaves numerous, 0.5–2.5 dm. long, evergreen, more or less decumbent, in basal rosette; hood globose, keel-shaped or pointed toward ventral edge of leaf, numerous small, colorless, opaque patches on dorsal curve of hood; orifice small, round, lateral, completely covered by expanded hood; wing usually prominent, broadest just above the middle; leaves green, variegated more or less heavily with red. Scape erect 2–3.5 dm. tall. Sepals ovate 2.0–2.5 cm. long, obtuse, green or dark red on outside; petals 2–4 cm. long, obovate, apex rounded or retuse, maroon; style disk 2–3.5 cm. in diameter, lobes 2-cleft. Mature capsule 5–12 mm. in diameter.

Type locality: "Ab urbe Augusta Georgiae ad Floridam."

Range: Fairly plentiful in bogs and open lowlands south of the Savannah River in Georgia, all of northern Florida, and west through southern Alabama into Mississippi and Louisiana.

Representative specimens: GEORGIA. Millen, Jenkins Co. *Wherry* (PENN); Coolidge, Thomas Co. *Coker* (CNC 31305). FLORIDA. St. James Island, Franklin Co. *Correll 5660*; Bloxham, Liberty Co. *Bell 535* (CNC); Milligan, Okaloosa Co. *Macfarlane* (PENN 49324). ALABAMA. Bay Minette, Baldwin Co. *Macfarlane* (PENN 38490); Theodore, Mobile Co. *Bell 534* (CNC). MISSISSIPPI. Ocean Springs, Jackson Co. *Pollard* (US 271560); Biloxi, Harrison Co. *Tracy* (US 341105). LOUISIANA. Covington, St. Tammany Co. *Peterson* (NY), also *Arsine* (US 1031876).

Since *S. psittacina* has a somewhat restricted range of latitude, its blooming season is likewise limited, beginning about April 1 and reaching its peak the last two weeks of that month. Its main blooming season is thus slightly later than those of *S. flava*, *S. Sledgei*, *S. Drummondii*, and *S. purpurea* in the same area.

The flowers of this species are consistently of the same shade of red or light maroon as those of *S. rubra* and do not show the effect of varied light intensities as do many of those of *S. purpurea*. The leaves, however, do show the effect of strong sunlight. Leaves of plants growing in shaded locations tend to be longer, greener, and have smaller hoods than those grown in the sun, which are

often found with large hoods and almost solid red leaves. The Okefenokee Swamp habitat has produced at least one extreme plant of *S. psittacina* as well as the large plants of *S. minor*. The specimen of *S. psittacina* above cited has long, slender leaves, one reaching a length of 27 cm. (Chesser Prairie, Okefenokee Swamp, Georgia, *F. Harper* (PH 768769)). The expanded hood of *S. psittacina* is very much like that of *Chrysamphora californica*, lacking only the two-winged appendages of the latter to be its duplicate in form. The orifice of the narrow pitcher of *S. psittacina* differs from that found in any other species of the genus in that it is lateral rather than terminal. This modification would seem to reduce the chances for the insect to escape when once inside the leaf.

Although the range of *S. psittacina* is not too extensive, it is coincident with parts of the ranges of every other species of the genus except *S. oreophila*. Despite this broad association and the lack of positive isolating mechanisms (*S. psittacina* has been crossed with *S. Drummondii*, thus uniting the morphological extremes of the genus), only one natural hybrid has been reported with *S. psittacina* as a parent. See section on natural hybrids, *S. minor* x *psittacina*.

8. **Sarracenia purpurea** L. Sp. Pl., p. 510. 1753.

Sarazina gibbosa Rafinesque, Autikon Botanikon, p. 33. 1840. Type loc. Canada to Virginia, swamps.

Sarazina venosa Rafinesque, Autikon Botanikon, p. 33. 1840. Type loc. Virginia to Florida.

S. purpurea var. *typica* Macfarlane, in Engl. Das Pflanzenreich **4**, pt. 110:33. 1908. Type loc. Manitoba to Florida.

S. purpurea venosa (Raf.) Wherry, Bartonia **15**: 3. 1933.

S. purpurea gibbosa (Raf.) Wherry, Bartonia **15**: 5. 1933.

Leaves evergreen, all of one type, 0.5–3.5 dm. long (or to 4.5 dm. in extreme cases in which event the petiole is long and slender, the pitchered portion of the leaf being the distal half only), decumbent, disposed in basal rosette, green, often more or less variegated with purple-red, but rarely clear yellow-green; pitcher ventricose; ventral wing widest near middle; orifice completely exposed due to erect position of the broadly cordate, repand hood. Scape erect, 1.5–4 dm. tall. Sepals maroon, green or yellow, ovate, 2–4 cm. long, never strongly recurved; petals more or less maroon, rarely yellow, fiddle-shaped, 4–6 cm. long, obtuse; style disk 3–4 cm. broad, the lobes notched. Mature capsule 1–2 cm. in diameter.

Type locality: "Hab. in Americae septentrionalis udis."

Range: Peat bogs from east central Canada to Pennsylvania and Maryland: low open pinelands of Virginia, North Carolina, northeastern half of South Carolina, and bordering the Gulf of Mexico in Georgia, northern Florida, Alabama, Mississippi, and Louisiana (?).

Representative specimens: (The symbol (S) is used to indicate plants from the northern range of Wherry's geographic subspecies that have the foliage characteristic of the southern subspecies; (I) indicates leaves intermediate between northern and southern type of plant as listed by Wherry.) SAS-

KATCHEWAN. Lake Athabaska, *Raup 6974* (NY). ONTARIO. (S) Sauble Beach, Lake Huron, *Wherry* (PENN); (I) Peterboro, Peterboro Co. *Wherry* (PENN). QUEBEC. Grindstone, Grindstone Island, *Fernald* (PH 734614); St. Jean Sur Le Lac, La Belle Co. *Pennell* (PH 737460); Roches Lake, Quebec Co. *Marie-Victorin* (US 872545). LABRADOR. (I) Northern Labrador, *Kenaston* (US 3021). NEWFOUNDLAND. (S) Whitbourne, *Robinson & Schrenk* (US); Exploits River Valley, *Fernald* (NY). NOVA SCOTIA. (S) Canso, Guysborough Co. *Fowler* (US 432916); Young's Lake, Annapolis Co. *Bell 561* and *562* (CNC); (S) Tiddville, Digby Co. *Fernald & Long* (PH 588448). MINNESOTA. (I) Duluth, St. Louis Co. *Lakela 2983* (PENN); Benedict, Hubbard Co. *Bergman 3046* (PENN). WISCONSIN. Eagle River, Vilas Co. *Lyon* (US 1630725); Marshland, Buffalo Co. *Holzinger* (PENN). MICHIGAN. (S) Manistique, Schoolcraft Co. *Pennell* (PH 764941); (I) Cecil Bay, Emmet Co. *Ehlers* (PH 655618); Haslet, Ingham Co. *Yunker* (US 1200855). ILLINOIS. Chicago, Cook Co. *Jaeger* (PH 752279). INDIANA. Leesburg Swamp, Kosciusko Co. *Wann* (PENN); Mineral Spring Station, Porter Co. *Wherry* (PENN). OHIO. (S) Canton, Stark Co. *Stair* (NY); (S) Silver Lake, Logan Co. *Stair* (US 310919). PENNSYLVANIA. (S) Lehigh Pond, Wayne Co. *Adams 3711* (PENN); (I) Gelatt, Susquehanna Co. *Glowenke 2302* (PENN). NEW HAMPSHIRE. Shelbourne, Coos Co. *Moore 4132* (PENN); Indian Pone, Grafton Co. *Reed* (DUKE 24656); (S) Petersborough, Hillsborough Co. *Batchelder* (PH 546097). VERMONT. Garden of Eden, Lamoille Co. *Knowlton* (PH 562838); Peacham, Caledonia Co. *Stevens* (US 310915). NEW YORK. (S) Argyle, Washington Co. *Schaeffer* (PH 791260); Cragsmoor, Ulster Co. *Farr* (PENN 46926); Conquest, Cayuga Co. *Wiegand* (PH 674040). MASSACHUSETTS. (S) Canton, Norfolk Co. *Standley & Blake* (US); (S) Petersham, Worcester Co. *Hough* (PENN); (S) Provincetown, Barnstable Co. *Fernald & Long* (PH 582163). MAINE. Arson Is., Oldtown, Penobscot Co. *Fernald & Long* (PH 574698); North Berwick, York Co. *True 213* (PENN). CONNECTICUT. (S) Eagleville, Tolland Co. *Travis 1960* (PENN); East Thompson, Windham Co. *Beals* (PH 618345). RHODE ISLAND. (S) Quidneset Point, *Bennett & Bailey* (DUKE 76047). NEW JERSEY. Green Pond, Warren Co. *Fritz* (PH 555546); Toms River, Ocean Co. *Bell 567* (CNC); Porchtown, Salem Co. *Foag 7071* (PENN). DELAWARE. Concord, Sussex Co. *Fisher* (PENN). MARYLAND. (S) Sharptown, Wicomico Co. *Wherry* (PENN); (S) Laurel, Prince George Co. *Marshall* (US 310917). VIRGINIA. Brunswick Co. *Va. Acad. Sci. Party* (PENN). NORTH CAROLINA. New Bern, Craven Co. *Radford & Stewart 1118* (CNC); Wilmington, Brunswick Co. *Radford 657* (CNC); Method, Raleigh, Wake Co. *Godfrey 3778* (CNC); Rocky Face, Alexander Co. *Totten* (CNC 3099); Cuba, Rutherford Co. *Lynch* (CNC 31347); Highlands, Macon Co. *Coker* (CNC 31348). SOUTH CAROLINA. Hartsville, Darlington Co. *Smith 877* (CNC); Georgetown, Georgetown Co. *Coker* (CNC 3106); Poinsett State Park, Sumter Co. *Blomquist & Holloway* (DUKE 53367). GEORGIA. Rabun Bald, Rabun Co. *Pyron* (DUKE 55857); Tattnall

Co. *Harper* 2151 (US). FLORIDA. Myron, Calhoun Co. *Moldenke 1158* (PENN); Fountain, Bay Co. *Bell 580* (CNC). ALABAMA. Bay Minette, Baldwin Co. *Bell 579* (CNC); Theodore, Mobile Co. *Bell 578* (CNC). MISSISSIPPI. Orange Grove, Jackson Co. *Oosting* (DUKE 49605).

S. purpurea, known in print since 1601, and the species upon which the genus was founded, is probably not the most numerous in number of individual plants since it does not occur in the large "*Sarracenia* meadows" of thousands of plants as do some of the other species; but it is by far the most widespread, being found, roughly speaking, from the subarctic to the sub-tropics, and extending sporadically near its northern limits from longitude 60° west to longitude 95° west. It blooms at the southern limits of its range the last two weeks of March and at proportionately later dates further north, blooming the last of August at the northern limits of the range. The flowers range in color from light red-purple (with green sepals) to extremely dark flowers in which both petals and the outer surface of the sepals are a very dark rich maroon. Although Wherry (1933) in delimiting the two subspecies of *S. purpurea* assigns the lighter colored flowers to the southern subspecies, the plants that produced the darkest flowers observed in the field in the present study were from near Bay Minette, Alabama (*Bell 2-30*). They were in full sun, as have been most other very dark red-flowered plants of this species observed. The only two plants of *S. purpurea* observed with uniformly dark red foliage were collected near White Lake, North Carolina, from a low area fully exposed to the sun and surrounded by pure white sand. These plants had very dark red blooms, but when brought into a more shaded location in the greenhouse subsequent blooms and foliage were observed to have noticeably less red pigmentation. This duplicated the observations of Macfarlane (1908) who noticed that plants growing in less open situations (or possibly only in cooler ones) usually have less red pigmentation in the leaves and tend to have lighter blooms than those plants of this species grown in full sun. In this connection a plant of *S. purpurea* similar to one discovered by F. M. Jones near Theodore, Alabama, in 1910 and described as a "color form" or mutant by Wherry was collected (*Bell 2-12*) during some recent field work near Fountain, Florida. The plant had light green sepals, pink petals and a pure white style disk. It was growing in a sphagnum clump in a densely shaded magnolia swamp. Other collections and field observations indicate that there is a direct relation between sun (and possibly temperature) and the degree of red pigment in plants of *S. purpurea*, the plants in full sun having redder foliage whenever the plant is genetically capable of the production of red pigmentation. No case has been found where plants of this species growing side by side in a given habitat will have leaves at the two extremes of the color range, i.e. solid green or solid red, as is often found in certain growths of *S. flava*.

The other characteristic used by Wherry for his subdivision of the species was leaf form, which appears none too constant in various herbarium specimens. The characteristic leaf type "the hollow part averaging over three times as long as wide; hood relatively small, its wings, when laterally flattened, extending little if at all beyond the pitcher-lip," which was assigned to the northern subspecies

S. purpurea gibbosa by Wherry (1933), is also found among plants in the southern areas of the range of *S. purpurea*, especially in the piedmont and mountains of North Carolina where ecological conditions approach, somewhat, those of higher latitudes. Peat bogs, which usually foster such variations as Wherry ascribes to the northern subspecies, are far more common in the north than the coastal plain savannah type of bog and therefore might possibly be the sole factor causing the modification of leaf characters. Appropriate reciprocal transplants will be made, but meanwhile the growth of the two types of *S. purpurea* under uniform conditions in the greenhouse may give a hint as to the outcome of the reciprocal transplant experiment. If the elongate leaf shape then remains constant on the northern long-leaved plants and if the seed collected in the field from such plants produces more long-leaved *S. purpurea* it will then have been proved that the characteristic is genetic rather than ecological. In such a case the two subspecies of Wherry would seem justified. However, it appears at this time that the minor differences between specific plants of *S. purpurea* are more environmental than hereditary, plants of a given morphological form being found throughout the entire range wherever the proper ecological factors necessary for its expression are found. Also many plants with intermediate leaf forms, or with leaves on the same plant definitely of both forms, are found throughout the range of this species, especially the northern range. For this reason the species is not considered here to be made up of two geographic subspecies, note being made, however, as to the extreme length often, but not always, attained by some plants from various localities, especially those in the higher latitudes.

In the southern portion of its range, from Virginia southward, *S. purpurea* grows at one station or another with every other species of *Sarracenia* except *S. oreophila*. Three different natural hybrids involving *S. purpurea* as a parent have been previously reported; and what is probably a new one is reported for the first time in the section of this paper on natural hybrids. See *S. purpurea* x *flava*, *S. purpurea* x *rubra*, *S. purpurea* x *Drummondii*, *S. purpurea* x *Sledgei*. and *S. purpurea* x *rubra* forma *jonesii*.

8-a. **Sarracenia purpurea** forma **heterophylla** (Eaton) Fernald, Rhodora **24:** 174. 1922.

S. heterophylla Eaton, Manual of Bot. for N. A. ed. 3, p. 447. 1822. Type loc. In swamps, Northampton, Mass.

S. purpurea heterophylla (Eaton) Torrey, Rept. Bot. Dept. Survey N. Y. Assembly No. 50: 120. 1839.

Differs chiefly from *S. purpurea* in that the flowers are yellow, and the leaves lack any trace of red, being yellow-green; the hood especially often turning a rich gold at maturity.

Type locality: In swamps, Northampton, Massachusetts.

Range: In small isolated colonies in Newfoundland, Nova Scotia, and possibly Massachusetts and New Jersey. Rare, except at locality given by Fernald in recognizing the plant as a form.

Representative specimens: NEWFOUNDLAND. Main Arm, Bonne Bay, *Fernald & Long* (PH 803203); Exploits River and Badger Brook, *Robinson & Schrenk* (US 217053). NOVA SCOTIA. Young's Lake, Belle Isle, Annapolis Co. *Fernald* (PH 588937), also *Bell 557* (CNC). NEW JERSEY. Forked River, *Britton* (NY).

This plant is here restored to the rank given it by Fernald in 1922 mainly because field observations and a review of the literature and herbarium material indicate it to be a small but constant and definite breeding entity of limited geographical range clearly within the structural and distributional limits of *S. purpurea*.

It was first named and described by Eaton in 1822 from a locality in Massachusetts. He termed it "A remarkably distinct species, but very rare." Later workers have variously reduced the rank of the plant from species to subspecies to variety to form to mutation, and finally Wherry (1933) has split the plant, considering the leaves to be "a slender-leaved ecad" and the flower "an anthocyan-free mutation."

Fernald in his "Notes on the Flora of Nova Scotia" says that the plant "occurs abundantly at the boggy margin of Young's Lake, . . .". This is indeed true, the plant being present in relatively large numbers and growing side by side with plants of *S. purpurea* that have leaves typically red or red-green. The degree of red coloration in these plants varied, but even where it was almost absent the leaves did not have the peculiar yellow hue so characteristic of forma *heterophylla*. This yellowness is almost lost when specimens are pressed. Therefore identification of pressed material is often difficult or even impossible, the pure green leaves of "shade grown" *S. purpurea* often appearing like the yellow-green leaves of the form when pressed. One thing can be used in a negative way, however, since *any* trace of red in the leaves *or* petals immediately prevents it from being classed as forma *heterophylla*. This point invalidates most of the *S. heterophylla* collected by Schallert in eastern North Carolina. The remaining plants so labeled, although showing no red, are therefore discounted as probably "shade plants."

In reinstating Fernald's form of *S. purpurea* the author does so with the feeling that it may actually deserve higher taxonomic rank. This is not just because the flower is reported to be yellow, but because it is felt that a plant which has through some evolutionary process evolved completely away from not only a specific but even a generic or possibly family characteristic (the production of anthocyans), and has become established as a breeding entity in an area already populated by another successful member of the genus, should have taxonomic importance. To call such a plant an anthocyanin-free mutation is proper so long as only one or two individuals occasionally occur and do not become established. But when such a "mutation," as it might well be, becomes a definite, reproducing (and probably geographically expanding) unit of the species population it should have recognition. Although its initial range is small, such a plant in following the cycle of mutation-reproduction-establishment is following one basic path toward speciation and should not be left out of consideration.

HYBRIDS IN NATURAL POPULATIONS

Although Harper (1918) reported some hybrid *Sarracenia* plants growing in localities isolated from the suspected parent forms, one would be safe in assuming that the first requirement for hybridization of these plants would be that the parent types involved in the cross grow more or less in the same local area. The fulfillment of this requirement, of course, does not guarantee that hybrids of the parent species will occur, as there are often physiological and/or morphological barriers between two species of the same genus. Such isolating mechanisms, however, are extremely weak or as yet not developed in most of the members of the genus *Sarracenia*; and as a result, geographical isolation seems to be the only truly effective barrier. The only species not found to be the parent of at least one hybrid is, therefore, *S. oreophila* which has a range completely isolated from other members of the genus. *S. purpurea*, on the other hand, is the recognized parent of five natural hybrids, and as might be suspected, has the most general and extensive range of any *Sarracenia*. If *S. purpurea* is the most evolved form, as suggested by Russell (1919), it would appear that little if any of its evolutionary capabilities have been used to develop positive isolating mechanisms. *S. flava* is involved in only three natural crosses, but it seems to cross readily when under cultivation as do all other species of *Sarracenia*. Note the following cross reported by Macfarlane (1908): [(*purpurea* x *flava*) x *purpurea*] x (*purpurea* x *psittacina*). Offspring of natural backcrosses have been observed and reported by Macfarlane, Harper, Russell, Wherry, and others. The first two noticed and reported on the intermediate character of *Sarracenia* hybrids, and in 1919 Russell published a paper on the comparison of hybrids with their parents. The summary was, in brief, that the hybrids are not only intermediate between the parents in grosser morphological characteristics, but also, with few minor exceptions, are intermediate in cellular detail as well. There appears to be no case of complete dominance in any hybrid, parental characteristics being visible after backcrosses as well as crosses.

Macfarlane found one hundred and seventeen plants of *S. purpurea* x *flava* in one day in Holmes county, Florida, which probably sets a record for that particular combination; but the most numerous hybrid is probably *S. Drummondii* x *Sledgei*. These two species overlap in southwestern Alabama between Mobile and the Alabama-Mississippi line, and within this area are actually thousands of these hybrids as well as all possible backcrosses. *S. Drummondii* and *S. Sledgei* interbreed as freely as if they were of the same species despite their morphological differences, and this may lead in time to the development of a new species in this locality. The first requirement of any such species would be a positive isolating mechanism. Otherwise its identity would soon be lost, due to the extreme gene flow between the parent plants under consideration in this area.

Unless the yellow form of *S. purpurea* occurred in a small population of *S. purpurea* or unless it quickly developed an isolating mechanism, it seems likely that it would have lost its identity.

The close relationship of the members of the genus *Sarracenia* is accentuated

by their ability to interbreed, and taxonomic problems are complicated by the resulting slow differentiation along various lines of evolution.

Since thirteen different natural combinations have been reported and since these hybrids are not too uncommon and can be recognized as definite units in the population, they are treated briefly here. The dozens of horticultural hybrids that have been reported are omitted. However, the most generally accepted horticultural name applied to any particular hybrid has been listed. Such names usually were applied to specific horticultural hybrids before the wild hybrid of the same parentage had been reported. No attempt has been made to record other horticultural data; and the order in which the natural hybrids are listed follows no special sequence, this order merely being most convenient for the author. Recognition is given to the first person to find and report each hybrid, and subsequent reports have not always been listed in this paper if the hybrid appeared to be more or less common.

Although there is no dominance involved in such hybrids, the gibbous character of *S. purpurea* is usually immediately evident, as is the white, undulate hood of *S. Drummondii*. For this reason they are listed first in any cross between them and any other species.

Conspicuous by their absence are reported natural hybrids of *S. Drummondii* x *psittacina*, *S. Drummondii* x *minor* and *S. minor* x *purpurea*, all of which have been made under cultivation, and all of which are possible as far as coincidence of range is concerned. Perhaps they will be reported in the future.

S. purpurea x *flava* = Catesbaei. *Macfarlane*, Wilmington, North Carolina, 1893; also *Macfarlane*, Holmes Co., Florida, and Baldwin Co., Alabama, 1905; *Bell*, Burgaw, North Carolina, 1947. Leaves similar in general shape to *S. purpurea* but longer, narrower; larger cordate erect hood. Flower intermediate red and yellow shaded together. Ponce de Leon, Holmes Co., Florida, *Macfarlane* (PENN 38475).

S. purpurea x *psittacina* = Courtii. Russell (1919) lists it as a reported natural hybrid but gives no further information or a description. Macfarlane (1908) never saw one growing wild. Cultivated in England, *Harrison* (US 2997).

S. purpurea x *Sledgei*. Russell (1919) reports it as grown in the University of Pennsylvania greenhouse, no further data. One plant collected near Theodore, Alabama, growing with its parents (*Bell 2-29*). Similar to the hybrid *S. Catesbaei*. Theodore, Mobile Co., Alabama, *Bell 542* (CNC).

S. purpurea x *rubra* = Chelsonii. Russell (1919) lists it as grown in University of Pennsylvania greenhouse, no further data. Wherry reported it collected in southeastern North Carolina, 1933. One plant from Scotland Co., North Carolina, collected in 1947 is growing in the University of North Carolina greenhouse. Leaves similar to *S. rubra*. Hood erect, larger than *rubra*, pitcher more expanded. Flower deep red, odorless. Sampson Co., North Carolina, *Wellman* (CNC). (Plate 13, fig. 6).

S. purpurea x *Drummondii* = Mitchelliana. *Macfarlane* (1908), Baldwin Co., Alabama, 1905. Also found by *Harper* (1918) in Walton Co., Florida, in 1911. Also *Bell* (*2-19*), Baldwin Co., Alabama, 1948. (First artificial hybrid, described

in England in 1887.) Leaf in general shape like that of *S. purpurea* but straighter and longer. Hood erect, cordate, undulate, white blotches, variegated red. Flower nodding, maroon. Theodore, Mobile Co., Alabama, *Bell* (CNC). (Plate 13, fig. 1).

S. Drummondii x *flava* = Moorei. Harper may have collected this in 1895 near Americus, Georgia, but identification was not positive. Macfarlane's plants found near Bay Minette, Alabama, in 1905 were cited by Harper. Pitchers similar to those of *S. flava* but hood undulate, white-blotched. Flowers intermediate rose and yellow. Crestview, Okaloosa Co., Florida, *Macfarlane* (PENN 15348, 49353, and 49354).

S. Drummondii x *Sledgei* = areolata. Russell (1919) from Mobile, Alabama, westward for thirty miles. *Wherry* (1935) same locality. *Bell* (*2-20*) west of Mobile, Alabama, 1948. Leaf similar to *S. Sledgei* but with white blotches at top. Hood slightly undulate. Flowers yellow-pink, intermediate. Theodore, Mobile Co., Alabama, *Macfarlane* (PENN 49329), also *Bell 542* (CNC).

S. Drummondii x *rubra* = Readi. Mentioned as the possible parentage of some plants collected by Harper (1918) near Americus, Georgia, in 1895 and 1901. No description. Listed by Russell (1919) but also without description. Herbarium specimen shows leaves to be intermediate in form and color. Deer Park, Washington Co., Alabama, *Reade* (PENN 57859).

S. minor x *flava* = crispata. *Harper* (1918), Bulloch Co., Georgia, 1901, and in Coffee Co., Georgia, 1902. *Macfarlane* (1908), Summerville, South Carolina. Pitchered leaves similar to *S. flava*, hood intermediate between parents. Douglas, Coffee Co., Georgia, *Harper 1437* (NY).

S. minor x *psittacina* = formosa. *Harper* (1918), Colquitt Co., Georgia, 1902, and Coffee, Irwin (now Ben Hill) and Wilcox counties in 1904. Harper (1918) states that this is the most free-flowering of the hybrids. Leaves decumbent, length intermediate, wing broad, intermediate, beaked hood like that of *S. psittacina*. Pitchers white-spotted as in *S. minor*. Fitzgerald, Irwin Co., Georgia, *Harper* (NY).

S. flava x *rubra*. *J. T. Harriot*, Carthage, North Carolina. No previous published report. Sepals tinged red, leaf intermediate between suspected parents. Carthage, Moore Co., North Carolina, *Harriot* (PH 815520).

S. rubra forma *jonesii* x *purpurea*. *Wherry* (1934) listed it as hybrid *S. jonesii* x *purpurea venosa*, undescribed. Mountains of North Carolina, 1932.

(*S. flava* x *purpurea*) x *flava*. *Macfarlane* (1908), Ponce de Leon, Florida, 1908. Pitchers like *S. flava* but flower shows traces of *S. purpurea*.

SUMMARY

The two genera of Sarraceniaceae under consideration are cytologically as well as morphologically distinct. The unreduced chromosome number for *Chrysamphora* (previously unreported) is thirty, while that of all members of the genus *Sarracenia* (previously unreported) is twenty-six. Within the latter genus chromosome morphology is of no value in interspecific differentiation. Morphological characteristics alone indicate, however, that a slight change in

previous taxonomic treatment is in order. *S. jonesii* is therefore reduced to the status of a form of *S. rubra*; the two subspecies of *S. purpurea* are consolidated and Fernald's form of this species, *heterophylla*, is reinstated.

During the investigation a previously unreported natural hybrid in the genus *Sarracenia* was found. Color photographs of intraspecific color differences in foliage were obtained for *S. flava* and *S. purpurea*.

ACKNOWLEDGMENTS

The writer wishes to take this opportunity to thank Dr. J. E. Adams for his interest and help with this work, and Dr. E. T. Wherry of the University of Pennsylvania for his help, field directions, and hospitality.

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EXPLANATIONS OF PLATES

PLATE 8

Camera lucida drawings (3271×) and photomicrographs (1294×) of chromosomes in root-tip cells of:

1. *S. oreophila*
2. *S. flava*

3. *S. Sledgei*
4. *S. Drummondii*

PLATE 9

Camera lucida drawings (3271×) and photomicrographs (1294×) of chromosomes in root-tip cells of:

5. *S. rubra*
6. *S. minor*
7. *S. psittacina*
8. *S. purpurea*

Note: The genome shown of *S. rubra* contains the smallest chromosomes seen in any cell of any *Sarracenia* during this study. Those of *S. minor* are among the largest observed. Thus figures 4 and 5 represent extremes. Average chromosome length for *S. rubra* is 2.75 microns and for *S. minor* 2.86 microns—a difference of only .11 microns. The average chromosome lengths for all other species of *Sarracenia* fall between these two "extremes."

PLATE 10

Pollen-mother-cell smears from all species of *Sarracenia* showing reduced chromosome number. Camera lucida drawings 1367×, photomicrographs 809×.

PLATE 11

1. Petal outlines ½×) of all species of *Sarracenia*.
   1. *S. Sledgei*; 2. *S. rubra* forma *jonesii*; 3. *S. Drummondii*; 4. *S. rubra*; 5. *S. purpurea*; 6. *S. minor*; 7. *S. oreophila*; 8. *S. psittacina*; 9. *S. flava*.
2. Sepals of *S. purpurea*.
3. Sepals of *S. rubra* showing strong recurving.
4. Side and face view of leaves of *S. rubra*, ½×.
5. Side and face view of leaves of *S. rubra* forma *jonesii*. ½×.
6. Leaf comparison: *S. rubra* and *S. rubra* forma *jonesii* and intergrades, all ½×. Left to right:
   a. *S. rubra* forma *jonesii*
   b. *S. rubra* forma *jonesii*
   c. *S. rubra* (previously considered *jonesii* because of size)
   d. *S. rubra* forma *jonesii*
   e. *S. rubra* (intermediate)
   f. *S. rubra*
   g. *S. rubra* (intermediate)
   h. *S. rubra*
   i. *S. rubra*
   j. *S. rubra*

   (a, b, d leaves from plant sent from Greenville, S. C. *Bell* 2-35; c leaf from plant collected at Deerland, Fla., *Bell* 2-15; all others from one clone of *S. rubra* collected in Moore Co., N. C., *Bell* 2-3. This entire series of leaves was pressed, *Bell 575* (CNC).

PLATE 12

Map of *S. rubra* and *S. rubra* forma *jonesii* distribution and probable range. All marks are of cited specimens.

PLATE 13

1. *S. purpurea* × *Drummondii*-Mitchelliana, in greenhouse. Collected in Baldwin Co., Ala. March 1948. Some leaves and flower pressed, *Bell 548* (CNC).

2-3. Blooms of *S. Sledgei* showing recurving of petals. Collected in Mobile Co., Ala., March 1948. Bloomed in greenhouse.

4. *S. rubra* (*S. jonesii* Wherry) collected in Mobile Co., Ala. The shape of these leaves is identical with smaller plants of *S. rubra*, but because of its size the specimen was previously classified as *S. jonesii*.

5. *S. rubra* collected at Lakeview, Moore Co., N. C. Although the leaves are less than a foot tall they have somewhat of an "intermediate" appearance. *Bell 519* (CNC).

6. *S. purpurea* × *rubra*-Chelsonii. This plant was sent to Dr. W. C. Coker from Scotland Co., N. C. in 1947 by Mr. C. Wellman. It bloomed in the greenhouse in 1948. The flower and some leaves were pressed.

7. *S. purpurea* forma *heterophylla*. Collected at Young's Lake, Belle Isle, Annapolis Co., Nova Scotia. The yellow character of the leaves does not show in a photograph of this type, but the lack of red markings can be noticed.

8. *S. rubra* forma *jonesii*. Plant growing in greenhouse. Note smaller typical *S. rubra* type leaves in the center of the picture.

PLATE 14

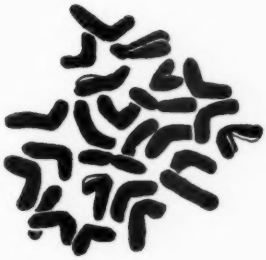
1. *Chrysamphora californica*. Photomicrograph of chromosomes in a root-tip section (1552×)

2. Camera lucida drawing (3925×) of material in 1 (above).

3. *Chrysamphora californica* growing in greenhouse.

PLATE 8

S. oreophila



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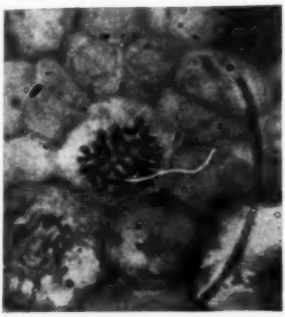
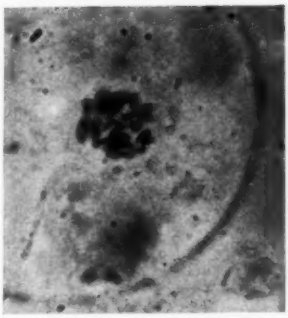


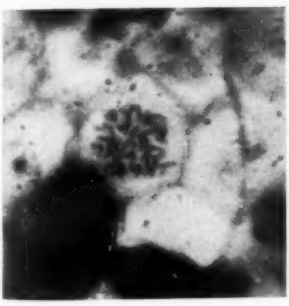
S. flava

2



S. Sledgei

3



S. Drummondii

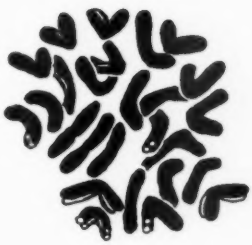


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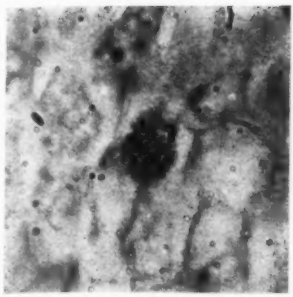
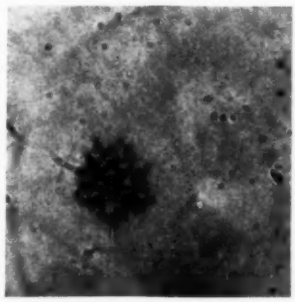
PLATE 9

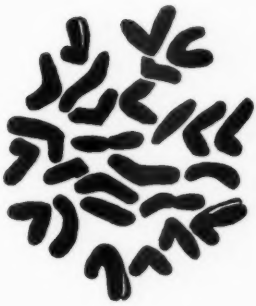


S. RUBRA

5



S. MINOR



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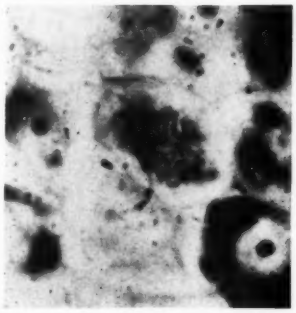
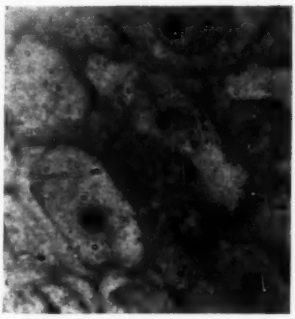
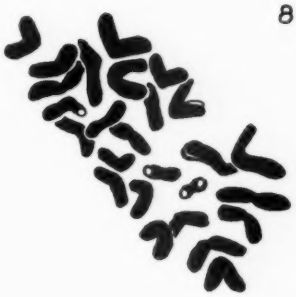


S. psittacina

7



S. purpurea



8

PLATE 10

1

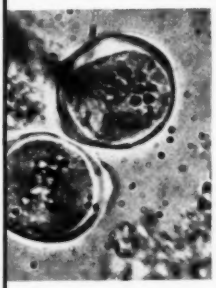
S. oreophila

2

S. flava

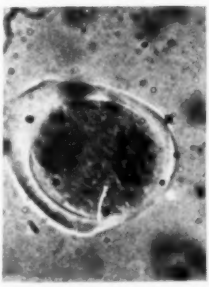
3

S. Sledgei



4

S. Drummondii

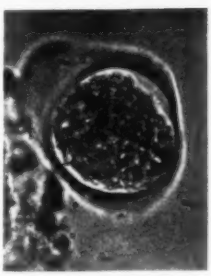


5

S. rubra

6

S. minor



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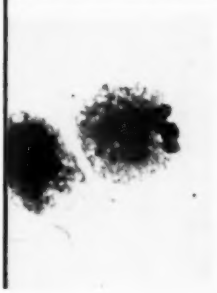
S. psittacina



8

S. purpurea

PLATE 11

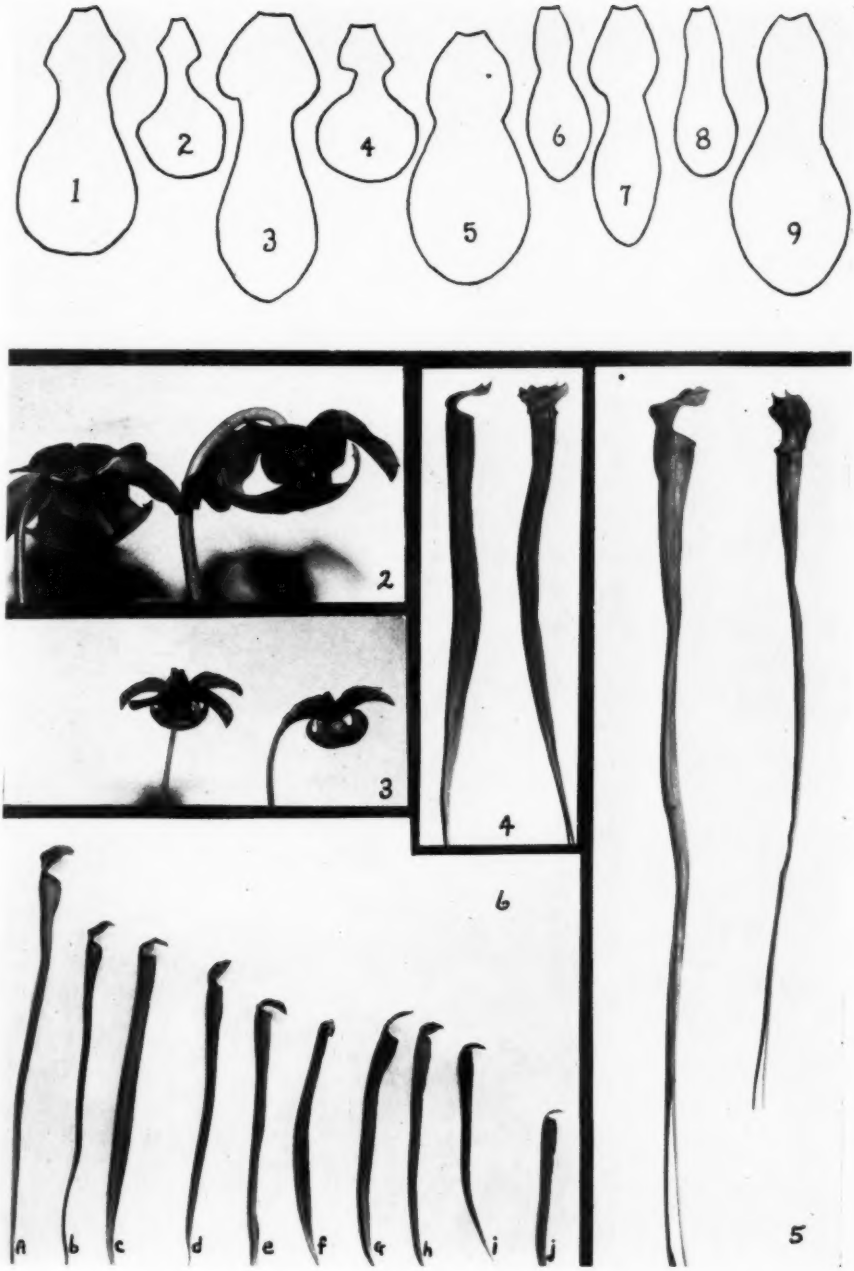


PLATE 12

Raleigh
Asheville
Wilmington
Florence
Atlanta
Montgomery
Waycross
Tallahassee
X S. RUBRA
Δ S. RUBRA form JONESII
--- RANGE

PLATE 13

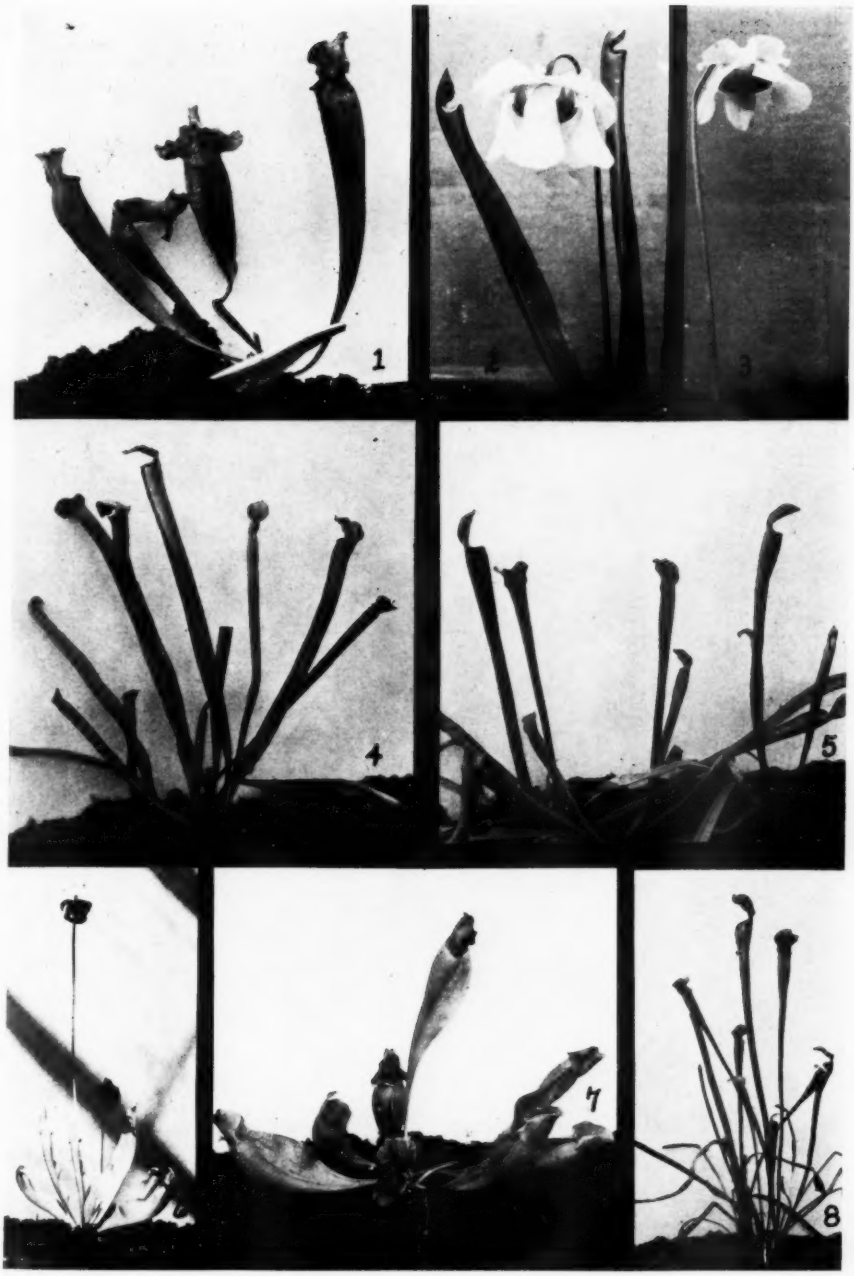
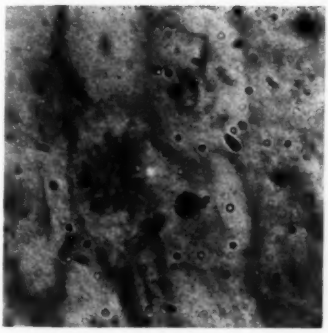
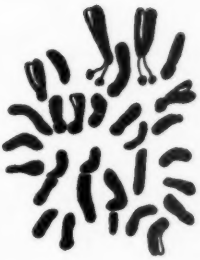


PLATE 14



1



2

3